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Aspects of variation in histology and cytology of the external nasal gland of Australian lizards

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Abstract

The histological and cytological structure of the external nasal gland was compared in 32 species of lizards representing the five families found in Australia. Considerable variation in the size of the gland was apparent, but size alone was not necessarily a reliable indicator of the gland's ability to function as an extrarenal salt-secreting organ. The elaboration of an hyperosmotic saline solution is associated with the presence of salt-transporting cells possessing a characteristic striated appearance, due to repeated folding of the basal and lateral membranes. These "striated cells" are generally grouped together into homogeneous tubular segments ("striated segments") which may occupy from 14% to 85% of the tubules in the gland depending upon the species. In the three large skinks studied, however, (*Egernia kingii*, *Tiliqua rugosa* and *T. occipitalis*) homogeneous "striated segments" do not occur, as salt-secreting and classical muco-serous cells intermingle throughout the length of the tubules and right up to the proximal end.

Nasal salt-secreting glands are most highly developed in the Australian Varanidae, and occur to some extent in all the Scincidae studied here. Salt-secreting elements occur rarely and then only feebly differentiated in the Australian Gekkonidae and Agamidae and are completely absent in the only member of the Pygopodidae examined, *Lialis burtonis*. External nasal glands in Australian lizards appear to differ from those described in species from both the Old and New World in that, even when apparently capable of functioning as salt-secreting glands, they show no obvious correlation with either environmental aridity or mode of nutrition.

Introduction

Recent studies have shown the lacertilian external nasal gland to be markedly polymorphic (Gabe & Saint Girons 1971, 1976; Dunson 1976; Lemire 1983). Often of small size and composed uniquely of classic glandular cells, it may also be enlarged and incorporate salt-secreting cells which are usually arranged in tubules having a characteristic striated appearance ("les segments striés" in the terminology of Gabe & Saint Girons, 1976). Although the mechanism of secretion is still not understood (Lemire 1983), it is clear that these cells are responsible for the capacity of these so-called "salt glands" to elaborate an hyperosmotic saline solution which, when eliminated, represents an important avenue of electrolyte excretion for many species. The presence and state of development of these salt-secreting cells appear to vary according to both the taxonomic position of the animal as well as its ecological situation.

From the literature it would appear that well-developed glands with striated segments are very common in the families Iguanidae and the Scincidae, frequent but more variable in their occurrence in the Varanidae, rare and very variable in their state of development in the Agamidae, absent or very little developed in the Gekkonidae and completely absent in the Chamaeleonidae and Anguioidea (including the Helodermatidae). By contrast, in agamids of the genus *Agama* and in the skink *Tiliqua rugosa* (Saint Girons, Lemire & Bradshaw 1977) the nasal gland is not

composed of typical homogeneous striated segments but, instead, salt-secreting cells are interspersed with classic glandular cells in the secretory tubules and are not restricted to an intermediary zone as in other species.

The ability of these glands to elaborate an hyperosmotic saline solution has been demonstrated unequivocally only in the case of the North African agamid lizard *Uromastix acanthinurus*, in about a dozen iguanids which are all herbivores and frequently desert-living or littoral species (see Lemire 1983 for references), and in three varanid species—one widely distributed in Australia (Green 1972), one littoral (Dunson 1974) and the other Saharan (Lemire 1983). In all the cases where the gland has been studied morphologically it is relatively large in size and packed with homogeneous striated segments representing from 65-95% of the total volume of the tubules.

Little is known of the physiology of "salt glands" from species where the gland is only moderately developed or where the salt-secreting elements form only 25-60% of the epithelium and the interpretation of data from such species is difficult (see Gerzelli & De Piceis-Polver 1970, Braysher 1971, Saint Girons *et al.* 1977, Minnich 1979). It does seem clear however that the small nasal gland of the Saharan *Agama* species has no osmoregulatory role, despite the fact that salt-secreting cells are common throughout the gland, intermixed with classical glandular cells (Lemire 1983). From a simple morphological point of view it is apparent that, within each Old World family, striated segments are more

common or more well-developed in species occupying arid regions and they are invariably highly developed in species which are primarily herbivorous.

The present investigation forms part of a detailed study of the ecophysiology of Australian reptiles, particularly lizards inhabiting arid and semi-arid regions of the continent (Bradshaw 1981, 1986) and an opportunity was taken to extend our limited knowledge of the morphology of these "salt glands" by examining common species living in a variety of habitats and representing the 5 families occurring in Australia.

MATERIALS AND METHODS

A list of the 32 species studied is given in Table 1. Amongst these, *Tiliqua rugosa* and the 4 varanids have already been the subject of detailed study (see Saint Girons *et al.* 1977, 1981). In the case of other species, specimens were autopsied the same day or the day following capture using Nembutal (Abbott, sodium pentobarbitone) as anaesthetic. The entire head was fixed for a period of 24 hr in aqueous Bouin, decalcified in 5% trichloroacetic acid, dehydrated and then blocked in paraffin. 10 µm serial sections were reconstituted in 6

series by mounting one section in every 10 or 20, depending upon the thickness of the head. These series were then stained successively with PAS-haematoxylin-picro indigocarmine, Gabe's Single Trichrome and Azan for topographic studies and with Mowry's PAS-alcian blue to detect mucins and with Danielli's tetrazoreaction for protids as described by Gabe (1976).

The volume of salt-secreting cells and striated segments, relative to either total cell volume or total secretory segments, and the relative size of the external nasal gland were estimated by eye following the method of Gabe & Saint Girons (1976). In addition, in those species where striated segments were quite distinct, photographs were made of the gland at three different levels, enlarged, and from these were cut all secretory segments both striated and glandular. These were then weighed to give an estimate of the relative proportion of salt-secreting to classical glandular portions of the gland. It should be emphasised, however, that it is possible to give a rough approximation only of the relative proportion of salt-secreting and classical glandular cells when both are interspersed all along the secretory tubules.

Table 1
List of species studied, habitat type and cytological and histological characteristics of the external nasal gland

Species	Habitat	Cell types		V1/V2*	Size of gland	Locality of capture of specimens
		C1	C2			
GEKKONIDAE						
<i>Crenodactylus ocellatus</i>	SA	MS	MS	0	2	NW W. Australia
<i>Diplodactylus stenodactylus</i>	SA	MS	MS	0	2	NW W. Australia
<i>Gehyra variegata</i>	A to H	MS	MS	0	2	Sydney
<i>Heteronotia binoci</i>	A to H	MS	MS	?	2	Alice Springs
<i>Oedura lesueuri</i>	SH	MS	MS	0	2	Sydney
<i>Rhynchoedura ornata</i>	A	MS	SM	0	2	NW W. Australia
<i>Underwoodisaurus milii</i>	M to SA	?	SM	0	2	Perth
PYGOPODIDAE						
<i>Lialis burtonis</i>	A to H	S	SM	0	3	Alice Springs
AGAMIDAE						
<i>Ctenophorus clayi</i>	A	SM	—	0	1	NW W. Australia
<i>Ctenophorus isolepis</i>	A	SM	—	0	1	NW W. Australia
<i>Ctenophorus maculatus</i>	SA	SM	—	0	1	NW W. Australia
<i>Ctenophorus ornatus</i>	M	SM	—	0	1	Perth
<i>Ctenophorus caudicinctus</i>	A	SM	—	0	1-2	NW W. Australia
<i>Ctenophorus nuchalis</i>	±A	SM	—	?	2	NW W. Australia
<i>Ctenophorus reticulatus</i>	±A	SM	—	?	2	Alice Springs
<i>Diporiphora australis</i>	H	SM	—	0	1	NE Queensland
<i>Lophognathus longirostris</i>	A	SM	—	0	1	Alice Springs
<i>Moloch horridus</i>	±A	SM	—	0	1	NW W. Australia
<i>Pogona minor</i>	A	SM	—	0	1	NW W. Australia
SCINCIDAE						
<i>Carlia fusca</i>	H	SM	MS	0.30	2-3	NE Queensland
<i>Carlia rhomboidalis</i>	H	SM	MS	0.38	2-3	NE Queensland
<i>Ctenotus taeniolatus</i>	H	SM	MS	0.32	2-3	NE Queensland
<i>Cryptoblepharus litoralis</i>	A to H	SM	MS	0.22	3	NE Queensland
<i>Egernia kingii</i>	M	MS	—	ca 0.3	2-3	Perth
<i>Hemiergis peronii</i>	M	SM	MS	0.47	2-3	Perth
<i>Menetia greyi</i>	±A	SM	MS	0.54	3	NW W. Australia
<i>Tiliqua occipitalis</i>	SA	MS	—	ca 0.3	2-3	NW W. Australia
<i>Tiliqua rugosa</i>	SA	MS	—	ca 0.3	2-3	Perth
VARANIDAE						
<i>Varanus giganteus</i>	A	SM	—	0.14	3	NW W. Australia
<i>Varanus rosenbergi</i>	M	SM	—	0.49	3-4	Perth
<i>Varanus acanthurus</i>	SA	SM	—	0.51	3-4	NW W. Australia
<i>Varanus gouldii</i>	A to H	MS	—	0.84	4	Perth

Habitat: A = very arid; ±A = more-or-less arid; SA = semi-arid; M = Mediterranean; SH = semi-humid; H = humid. For C1 and C2 cells, type of secretion: S = serous; SM = sero-mucous; MS = muco-serous.

*V1/V2 = Ratio of volume of striated segments (or salt-secreting cells) to total tubular volume (or total glandular epithelium).

RESULTS

The general structure of the external nasal gland of lacertilians has been described on a number of occasions and excellent reviews will be found in Parsons (1970), Dunson (1976), Gabe & Saint Girons (1976) and Lemire (1983). Amongst the Australian species listed in Table 1 the epithelium of the glandular tubules is always composed, other than for small dispersed basal cells, of large cubic or prismatic cells (C1) with a basal nucleus and classified by their secretions as either *sero-mucous* (i.e. PAS-positive and rich in protids but without acid mucins) or *mucoserous* (i.e. PAS-positive and containing both protids and acid mucins). Rarely these C1 cells may be serous only, that is, rich in protids but PAS-negative and without acid mucins. In the Gekkonidae these cells are mucoserous but differ in being very weakly PAS-positive and staining with haematoxylin. In the Agamidae the secretory tubules are composed completely of C1 cells but, in other species, these cells which are always preponderant in the upper portions of the tubules, may be replaced progressively by other elements in the middle and lower reaches of the tubules.

A second category of cells (C2) which is very evident in the Gekkonidae and most of the Scincidae is composed of either mucoserous or (only in some Gekkota) sero-mucous cells, with a basal nucleus and PAS-positive secretions. In the upper (blind) parts of the secretory tubules these cells are small in size, conical in shape and compressed between the large C1 cells. In the middle section of the tubules the C2 cells enlarge progressively, assume a cubic or prismatic shape and become proportionately more numerous. In most of the Gekkonidae these are the only cell types to be found in the proximal section of the secretory tubules but in most of the Scincidae they appear to metamorphose into salt-secreting cells starting in the middle sections of the tubules.

In the three large skinks (*Egernia kingii*, *Tiliqua rugosa* and *Tiliqua occipitalis*) and all the varanids, the small conical cells in the upper regions of the tubules (C2?) lack secretory products and their progressive transformation into salt-secreting cells is more evident. Once well-differentiated, these cells appear pyramidal or prismatic with a central clear ovoid nucleus and with a cytoplasm completely devoid of secretory material but filled with mitochondria. The extreme folding of the lateral cellular membranes, and often the basal membrane as well, confers on the epithelium of these cells a characteristic striated appearance when viewed under the light microscope (les "cellules striées" of Gabe & Saint Girons, 1976). In a more-or-less long transition zone, near the blind end of the secretory tubules, these salt-secreting cells in the process of differentiation are mixed with C1 cells. In the proximal section of the tubules the completely formed salt-secreting cells produce homogeneous striated segments in the Varanidae and *Menetia greyi*. In most of the Scincidae one can still talk of "striated segments", even though some C1 cells will be found in the epithelium, but in the three large skinks, salt-secreting cells and mucoserous cells intermingle right up to the proximal end of the secretory tubules, even though the salt-secreting cells become progressively more abundant.

In some cases the cellular composition of the epithelium is difficult to define precisely, at least under the light microscope, because of the gradual differentiation of the salt-secreting cells. In *Ctenophorus nuchalis* and *Ctenophorus reticulatus*, for example, the

mucoserous cells (C1) become taller with clearer nuclei sited further from the basal membrane in the proximal third of the secretory tubules, and their secretory products become less evident and finally disappear altogether so that the striated aspect of the epithelium is not at all clear. The same phenomenon, although a little less obvious, is also seen with *Ctenophorus caudicinctus*, and in *Heteronotia binocci* an analogous situation is seen in the proximal portion of the tubules.

Given the wide variations in head shape and nasal cavities from one Family to another, and even between related genera, it is difficult to arrive at precise figures for the relative volume of the external nasal gland in different species and this is further complicated by variations in the proportion of glandular tubules to conjunctiva. Gross comparisons are nevertheless possible, and the relative development of the gland is given for each species in Table 1 on an arbitrary scale from 1 to 4 with 1 being represented by most of the agamid species and 4 by *Varanus gouldii* which has an active salt-secreting gland.

DISCUSSION

The aim of this investigation was twofold: firstly to extend our very limited knowledge of the histological structure of the external nasal gland of Australian lizards and, secondly, to document variations in the relative abundance of salt-secreting elements in the glands of these lizards and to correlate these wherever possible with differences in ecology, geographic distribution or systematic position of the species concerned.

Our results confirm those of other workers and salt-secreting cells were found in all Scincidae; "striated segments" occurred frequently but showed variable development in the Varanidae and they occurred rarely and then were only feebly differentiated in the Gekkonidae and in most of the Agamidae. Striated segments were completely absent from the external nasal gland of the only member of the family Pygopodidae included here, *Lialis burtonis*. Taking into account the relative development of the salt-secreting cells, whether or not assembled into homogeneous striated segments, the lizards studied here fall into three separate groups. The first is represented by *Varanus gouldii* where striated segments constitute the major part of the gland (see also Saint Girons *et al.* 1981); the second by various Varanidae and Scincidae which all possess clearly-developed striated segments or numerous salt-secreting cells interspersed with classic glandular cells ("mixed" glands); and the third by the geckos, agamids and the pygopodids where salt-secreting cells are either absent or very rare and poorly differentiated when they do occur.

Within the Scincidae it is possible to distinguish a further three distinct groups according to the distribution of the salt-secreting cells within the gland. In *Scincus scincus* (Lemire 1983), *Chalcides mionecton* (Gabe & Saint Girons 1976) and *Menetia greyi*, which are all semi-fossorial species from more-or-less arid regions, there are two categories of classic glandular cells in the distal regions of the secretory tubules, whereas the middle and proximal regions are occupied by voluminous and homogeneous striated segments. Most of the Australian skinks fall into a second category which conforms essentially to this basic pattern but differs in a slightly lesser development of the striated segments and the fact that the mucoserous C2 cells occur scattered throughout the epithelium, right up to the level of the excretory duct. The third group is represented by the

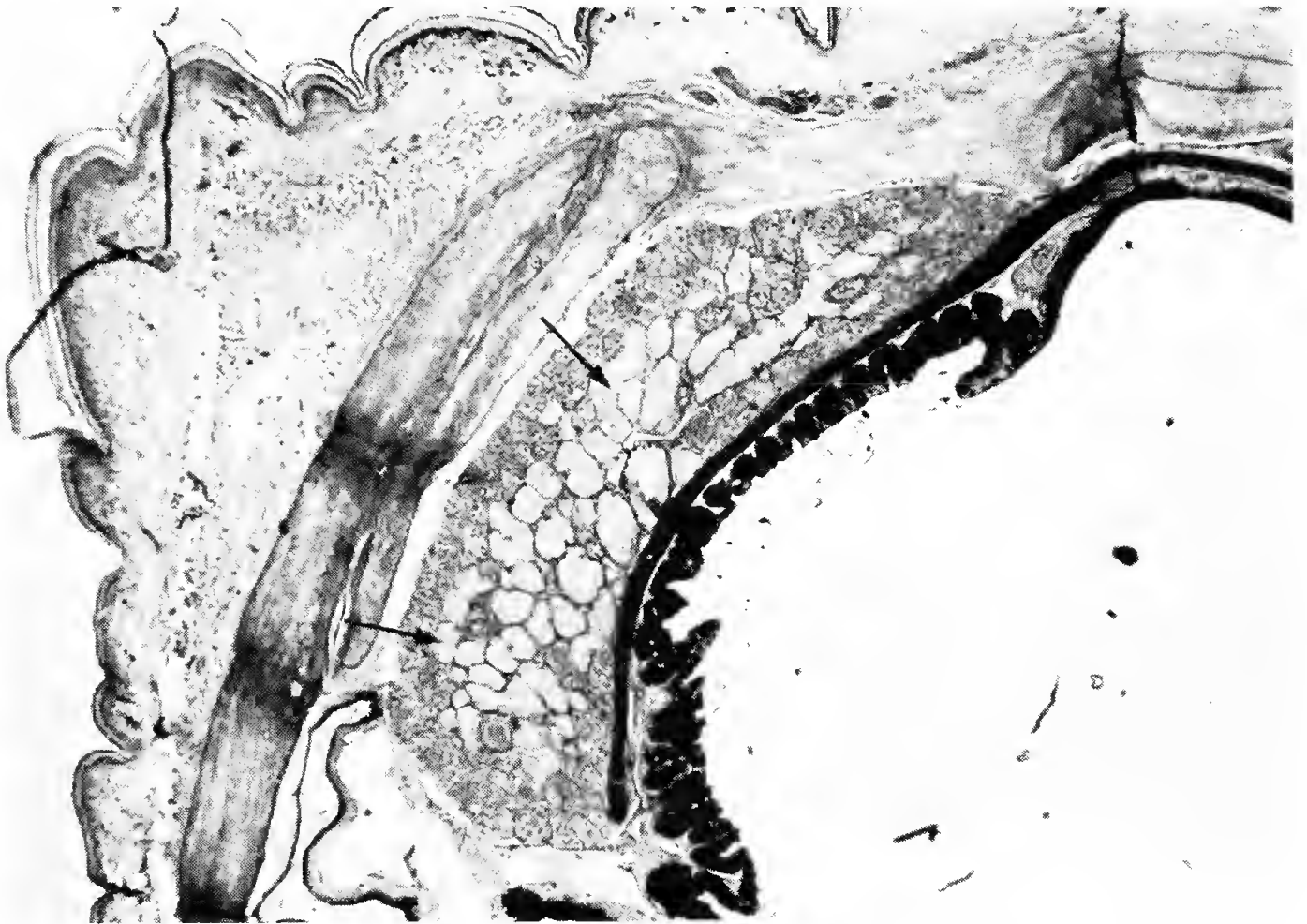


Figure 1.—Transverse section of the head of *Varanus acanthurus* at the level of the external nasal gland. Stained with PAS-haematoxylin-picro-indigocarmine, green filter x 50. "Striated segments" which are more voluminous and lack secretory products are indicated by arrows and are quite distinct from the classical glandular secretory elements.

three large skinks studied here (*Tiliqua rugosa*, *Egernia kingii* and *Tiliqua occipitalis*) where it is clear that even though the maturation of C2 cells into salt-secreting cells commences in the distal regions of the secretory tubules, homogeneous striated segments are never formed because C1 cells can still be found at the proximal extremity of the tubules. In contrast, the external nasal gland of the Australian agamids, although equally poorly developed, differs from that of the Saharan *Agama* (Lemire 1983) in that there is never a mixture of classical glandular cells and salt-secreting cells within the one tubule, and when the former develop into salt-secreting cells, they do so incompletely and only at the proximal extremities of the secretory tubules.

Cytological components associated with salt secretion assume an important proportion of the glandular tubules only when the nasal gland is well developed (2 in our classification) but large nasal glands are not necessarily dedicated to salt-secretion. In *Lialis burtonis*, for example, the external nasal gland is well developed (3) but contains no salt-secreting cells whatsoever. This highlights the difficulty experienced by many workers (ourselves included) in attempting to gauge the physiological potentialities of a given gland from its histological structure. There is no doubt that *Varanus gouldii*, which possesses a voluminous external nasal gland composed primarily of homogeneous striated segments, has the capability of elaborating an hyperosmotic saline solution and this has been

confirmed experimentally by Green (1972). It is highly probable that this same capacity is also shared by other lizards falling in the second group, such as *Menetia greyi*, *Varanus acanthurus*, *Varanus rosenbergi* and *Hemiergis peronii*, all of which live in arid and semi-arid regions throughout Australia. *Varanus gouldii* is distributed throughout the entire Australian continent and is found in desert as well as sub-humid forest situations but it is not known whether the nasal gland is equally developed in all individuals. Typically, the individuals which have been studied come from arid or semi-arid situations where one would expect, *a priori*, the gland to be well developed, and Green's animals (*op.cit.*) for example were collected in arid regions of South Australia. *Varanus rosenbergi* is more mediterranean in its distribution but is often found in littoral situations where salt intake would be expected to be elevated.

It is difficult to predict in the case of those other species falling in this second category—possessing salt-secreting cells either dispersed throughout the gland or forming almost homogeneous striated segments, but accounting for only 10-40% of the total volume of the secretory tubules—whether their nasal glands are capable of secreting an hyperosmotic solution. At least in the case of the skink *Tiliqua rugosa* which possesses such a "mixed" gland, it is clear from recent work by Bradshaw, Tom & Bunn (1984) that this lizard is capable of elaborating such a solution in response to electrolyte

loading with either NaCl or KCl and the fluid excreted from the gland has an osmotic pressure approximately 3.5 times that of the plasma. Further studies are needed urgently, however, in order to define the physiological capacities of these glands which, at first sight, would seem to lack the requisite development and organisation of salt-secreting elements required to elaborate a concentrated salt solution (Saint Girons *et al.* 1977).

When one looks for correlations between the development of the external nasal gland in the various species included in this study and their geographic distribution within Australia, none emerges. For example, the nasal gland of *Carlia rhomboidalis* is well developed with obvious striated segments and would appear, on histological criteria, capable of secreting a hypersaline fluid, but this species is localised in one of the wettest regions of Australia where it would not be expected to have any need of an extra-renal salt-secreting organ. *Varanus giganteus* on the other hand is found exclusively in the most arid regions of the continent and yet possesses a nasal gland in which striated segments are only very poorly developed and it would appear that, within Australia at least, nasal salt glands bear little correlation with environmental aridity. The other correlation noted in reptiles from both the Old and New World is herbivory, but none of the Australian lizards is an obligate herbivore, like for example the North African agamid *Uromastix acanthinurus*. The three large skinks studied here, which are all partially herbivorous (*Tiliqua rugosa*, *Tiliqua occipitalis* and *Egernia kingii*) show no greater development of salt-secreting elements in their external nasal glands than do insectivorous species.

Given the morphology of the external nasal glands of lizards falling in the third category, where salt-secreting cells are either absent or only marginally developed, any role of the gland in osmoregulation can be excluded. This includes all the species of the genus *Ctenophorus* studied, many of which live in particularly arid regions. This is consistent with what is known of the water and electrolyte physiology of these lizards which survive long periods of water deprivation through their ability to retain sodium ions in the body fluids at markedly elevated concentrations (Bradshaw & Shoemaker 1967, Bradshaw 1981, 1986). Lizards of the genus *Agama* living in the Sahara similarly tolerate hypernatraemia, rather than excrete sodium ions via an external nasal gland (Lemire 1983) and even *Uromastix acanthinurus*, which possesses one of the most developed external nasal glands of any lizard, has a very limited ability to excrete sodium ions as shown by the work of Bradshaw *et al.* (1984) and experiences hypernatraemia in its natural habitat during periods of water deprivation (Lemire *et al.* 1982). Amongst the *Ctenophorus* species examined here, only *caudicinctus* and *nuchalis* show any tendency towards development of salt-secreting cells in the nasal gland, as with *Heteronotia binocoi* amongst the geckos. The ecological and physiological significance of this is, however, obscure, particularly in the case of this gecko which has recently been shown to be parthenogenetic in parts of its range (Moritz 1983, 1984).

In conclusion, it would appear that ecological and environmental correlates with nasal gland development, particularly aridity and mode of nutrition, are much less obvious in Australian lizards than in other parts of the world. In part this may stem from our poorer knowledge of the ecology of many of these species and it would be most useful for future ecophysiological studies if the osmoregulatory capacities of these glands could be defined.

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Northern Sandplain Kwongan: regeneration following fire, juvenile period and flowering phenology

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Abstract

Fire is an integral factor in the ecology and management of the shrub lands of the Northern Sandplains in Western Australia. Documentation of fire effects on 192 species from a range of edaphic conditions revealed that 73% were capable of resprouting after fire. Both resprouting and reseeding species resumed flowering quickly following fire with 79% of the species flowering within two years. Particular species requiring longer juvenile periods, however, could have important management consideration due to their status as pollen species for apiculture or their conservation status. Flowering peaked in September in this study region and there were no major differences in phenology of more recently burned sites compared with mature shrublands. The interaction of the use of fire to protect human developments and the desired maintenance of areas of unburnt shrubland for honeybee pastures and biological species preservation is discussed.

Introduction

Fire is an integral factor in the shrub-dominated ecosystems throughout the world (Specht 1979). The plants of these communities possess numerous adaptations which enable them to regenerate after fire, such as sprouting from buds located in underground organs and fire-stimulated seed germination. Studies on the effect of fires on shrub-dominated heaths in Australia have shown that most of the species regenerate after fire by sprouting (Specht *et al.* 1958, Siddiqi *et al.* 1976, Russell and Parson 1978, Bell *et al.* 1984, Bell 1985). In these communities the species which lack the ability to resprout, i.e. obligate seeders, regenerate either by fire-stimulated germination of seed stored in the soil or by dispersal of seed held in woody fruits. The effect of fire on soil-stored seed is well documented (Stone and Juhren 1951, Went *et al.* 1952, Cushwa *et al.* 1952, Christensen and Muller 1975). The depth and intensity of heat through the soil profile during a fire is an important factor in determining post-fire regeneration (Shea *et al.* 1979). A very hot fire may kill underground organs (Hopkins 1979) and soil-stored seed, whereas a fire of low intensity may not stimulate some seed to germinate (McArthur and Cheney 1966).

Some Australian plant species, eg. *Xanthorrhoea* spp. and a few species of the Orchidaceae actually depend on fire to stimulate flowering (Gill 1975). Most plants, however, require a certain time after a fire before reproduction begins. This period, termed the "juvenile period", is least important for plants regenerating after fire by sprouting but is an important characteristic of plants regenerating from seed. Time since last fire may also have an impact on the annual period of flowering.

The Northern Sandplain shrublands have probably been subjected to periodic fires for at least the past 5 000 years (Churchill 1968). Under conditions prior to the

settlement of the region by European man, the region probably received fires on a cycle of some 25 years (Bell 1985). Today fire frequencies are higher due to man-caused fires (Bell *et al.* 1984) and a controlled-burning regime must be imposed on certain regions under management (Bell and Loneragan 1985).

Some of the Northern Sandplain shrublands have been reserved in National Parks and Nature Reserves, but extensive areas have been cleared for agricultural, pastoral and mining land uses. Uncleared land serves a number of economic purposes including the tourist industry and the cut-flower and native seed collection trades. The Northern Sandplain native shrublands also serve as winter season "honeybee pastures" for commercial apiarists. The beekeeping industry uses the native shrublands and especially the pollen produced by winter-flowering species to maintain hives and to build up worker bee numbers for the honey production seasons in the south-western forest regions later in the year.

Fire management in the Northern Sandplain must provide sufficient areas of prolific shrublands to serve the needs of commercial apiculture while protecting life and property in the adjacent wheat and pasture developments. Information on the impact of fires on the shrublands is of primary importance to the apiculture industry and aspects of species conservation. Conservation of community types and the flora and fauna of regions of this rich (Lamont *et al.* 1984) and highly endemic (Rye 1982) shrubland must also consider the impact of fire (Bell *et al.* 1984). The following study was designed to provide information on the influence of fire on the mode of regeneration, the length of the juvenile period and the flowering phenology for species of these Northern Sandplain shrublands.

Methods

Twenty-six permanently marked 20 m x 10 m plots were established in Northern Sandplain shrublands near Badgingarra, Western Australia (30°16'S, 115°26'E). The sites were representative of a range of topographic sites and ages-since-last-fire. Each site was initially categorized as lateritic upland or deep sand slope as these edaphic conditions have proved to produce the major floristic differences in the vegetation of this region (Bell and Loneragan 1985). The ages of more recently burned sites were determined by records of the Western Australian Bush Fire Board. Sites burned before 11 years ago could not be exactly documented and were grouped as >11 years. Each site was visited monthly from March 1981 till December 1981 and a list of species in flower was compiled.

Post-fire regeneration strategies were determined from recently burnt sites. Obligate seed regenerating species could be recognized because they initially have only a single erect stem. These seedlings were clearly differentiated from resprouting species which tend to be multi-stemmed. Geophytes were classed as sprouters since they regenerate after fire by producing new shoots from underground storage organs.

Results and Discussion

Resprouting after fire

During the study 238 species were identified (Table 1, Appendix 1). The range of sites allowed particular species to be assigned to edaphic preference categories. Among the 192 species identified in this way, approximately equal numbers were subjectively assigned to the generalist (or edaphically indifferent), lateritic or sand specialist categories. The vegetation patterns in the Northern Sandplain shrublands have previously been shown to correspond strongly to the major differences in soil conditions, but fire was also shown to influence the floristic composition of stands in these shrublands (Bell and Loneragan 1985).

Categorizing species of the Northern Sandplain study sites into mode of regeneration after fire revealed that 73% of the 192 species recorded in this way were capable of resprouting after fire. This division of sprouters and obligate seeders is similar to shrubland sites in eastern Australia where the reported percentages of sprouters includes 70% in South Australia (Specht *et al.* 1958), 73% in Victoria (Russell and Parsons 1978) and 80% for the coastal heaths of New South Wales (Siddiqi *et al.* 1976). The sclerophyllous shrub-dominated understorey of the jarrah forest of the Darling Range also contains a similar proportion of resprouting species (Christensen and Kimber 1975, Bell and Koch 1980). In a more limited study of predominantly deep sand sites in the Northern Sandplain, resprouter species represented 66% of the total (Bell *et al.* 1984).

Table 1

Summary statistics for the fire response survey in the Northern Sandplain shrublands near Badgingarra, Western Australia.

Total Species Identified in studies	Total			
	238			
Species Categorized for Edaphic Preference	Total	Generalists	Sand	Laterite
	197	72	61	64
Species Categorized for Regeneration Strategy	Total	Sprouter	Seeder	Both
	192	126	51	15
Species Categorized for Juvenile Period	Total	<2 yrs	>2<4 yrs	>4 yrs
	108	87	16	5
Species in Phenology Study	Total			
	149			

The "sprouting" habit is considered an adaptation to recurring fire (Biswell 1974). Conversely, a long fire-free period was probably important in evolving the obligate seeding strategy (Keeley and Zedler 1978). However, it is uncertain whether the characters such as sprouting, woody fruits and hard seeds are adaptations specifically to fire or adaptations to other environmental factors, such as a low nutrient regime (Specht 1979), drought (Hnatiuk and Hopkins 1980) or insect damage (Morrow 1977). Whatever their origin, these adaptations ensure survival in the fire-prone regions of the Northern Sandplain.

Many of the tall shrubs of the Badgingarra shrublands are obligate seeders, e.g. *Hakea obliqua*, *Adenanthos cygnorum*, *Dryandra sessilis*. This relationship of size with regeneration mode was also identified in Kings Park, Western Australia (Baird 1977). The significance of this relationship, however, is obscure. A number of the obligate seeders possessed the bradysporous habit (Specht 1979), i.e. seeds are retained in woody fruits or cones until a fire opens the fruit. Examples of species with this habit in Western Australian heathlands are *Hakea obliqua*, *Eremaea fimbriata* and *Beaufortia elegans*. Other obligate seeders such as *Acacia pulchella* and *Kennedia prostrata* possess "hard" seeds (Ewart 1908). These seeds remain viable and dormant for long periods in the soil until some event, usually fire, stimulates them to germinate. The effect of fire on these hard seeds is to crack the seedcoat making it permeable to moisture and oxygen (Beadle 1940; Floyd 1966, 1976). As hard seeds can remain viable in the soil for many years even after the parent plants have died, species richness and diversity often increases following managed fuel-reduction fires (Bell and Koch 1980).

Flowering phenology

Throughout the 26 shrubland sites the maximum flowering period occurred in spring with a peak of 74 species recorded on September 29th (Fig. 1, Appendix 1). Common winter flowering species were *Leucopogon conostephioides*, *Andersonia lehmanniana* and *Stylidium repens*. In late winter and early spring *Hibbertia crassifolia*, *H. hypericoides* and *Drosera heterophylla* were flowering abundantly in most sites. With the onset of spring many more species began their flowering period and no species dominated flowering throughout all sites. *Calothamnus sanguineus* was the only species which flowered throughout the sampling period.

The rapid increase in flowering species towards spring was associated with an increase in flowering for species of the families Myrtaceae and Proteaceae and a decrease in the Epacridaceae (Fig. 2). The winter maxima for members of the Epacridaceae are important as members of this family are reported to be favoured apicultural species (Smith 1969).

In comparing the flowering periods between sites varying in the time-since-last-fire, only two species, *Hypocalymma xanthopetalum* and *Hovea stricta* showed a different phenological pattern between the recently burnt and long unburnt sites. *Hypocalymma xanthopetalum* flowered in two year old sites as much as two months before it flowered in any of the older sites. *Hovea stricta* flowered in two- and five-year-old sites, also two months before it flowered in the greater than eleven-year-old sites. In general, however, stand-age had little relationship to the period of availability for honeybee use once the juvenile period was completed.

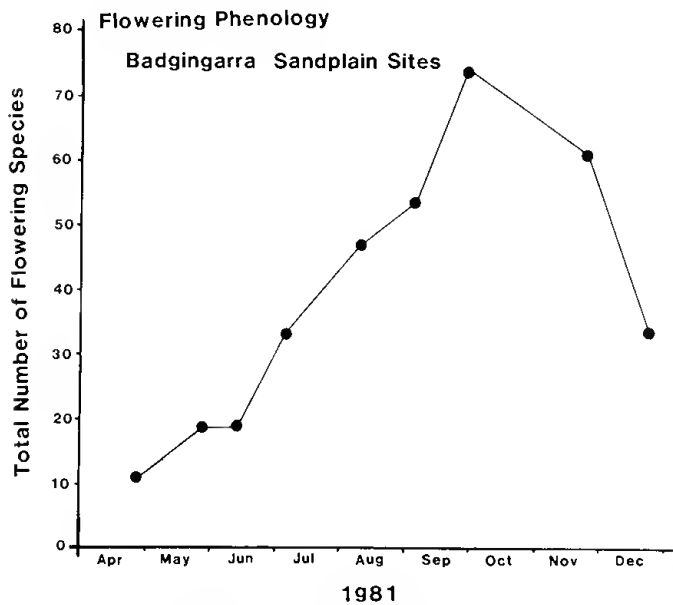


Figure 1.—Total number of species flowering in 26 heathland study sites in the Northern Sandplain during the period April through December 1981.

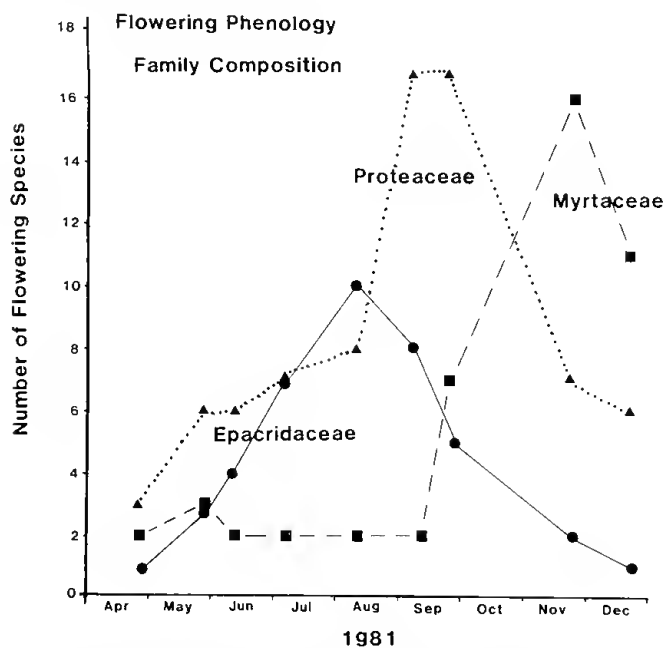


Figure 2.—Total number of Epacridaceae, Myrtaceae and Proteaceae species flowering in 26 heathland study sites in the Northern Sandplain during the period April-December 1981.

Several species flowered profusely in the first few years following a fire, but then were only minimally reproductive in older sites. The most conspicuous of these plants was *Verticordia grandis* which produced a mass of bright red flowers in the sites of less than two years old. The fire-stimulated success of species such as *Verticordia grandis*, *Stirlingia latifolia*, *Anigozanthos humilis*, *Pimelea sulphurea*, and others may be a response to light as observed by Stone and Juhren (1951) or induced by substances produced during a fire. Gill and Ingwersen (1976) demonstrated that injection of ethylene, which is produced in large quantities during a fire, into *Xanthorrhoea australis* stimulated the species to flower as it would normally do after a fire. Even though many plants flower only after a fire, there was no difference in the number of species flowering in burnt and unburnt sites (Table 2). The study of several sites over a period of years would probably show some pattern in the number of species flowering after a fire but in this study, the variation between sites of the same age was too great to permit valid comparisons between sites of different ages.

Table 2

Species in flower at each site for 1981 for the 26 Northern Sandplain kwongan study sites.

Site Number	Years Since Last Burn	Date 1981								
		29.4	28.5	10.6	7.7	5.8	1.9	29.9	20.11	19.12
Sand										
2	>11	0	1	1	5	5	7	—	6	4
14	>11	—	0	1	2	4	5	b	b	b
16	>11	—	1	1	2	4	7	8	11	7
21	>11	1	1	2	2	3	10	8	9	7
7	11	2	0	0	5	8	9	—	4	5
12	11	—	0	1	2	4	9	9	10	7
1	10	0	1	2	3	5	9	—	5	3
17	7	0	1	2	1	3	7	11	12	6
19	6	0	3	4	6	7	7	14	11	8
23	5	2	3	4	5	5	10	10	7	8
3	4	0	3	3	4	7	9	14	10	4
5	2	0	0	0	3	5	9	14	8	4
25	2	2	2	1	5	7	7	11	12	8
9	2	2	2	1	3	4	9	11	4	6
Laterite										
10	>11	—	2	2	b	b	b	b	b	b
13	>11	—	3	3	2	6	6	9	4	4
15	>11	—	3	3	6	8	7	9	6	4
22	>11	2	1	1	5	10	9	20	9	6
8	11	0	1	2	5	9	13	b	b	b
18	7	0	0	1	8	12	7	10	5	1
20	6	0	1	3	3	8	4	10	5	6
24	5	1	1	3	5	9	7	13	8	4
4	4	0	1	2	5	9	6	11	4	4
6	2	0	1	2	4	8	8	11	8	4
26	2	0	0	0	7	10	8	16	9	4
11	2	—	1	—	1	4	5	10	7	5

b = burnt

— = unsampled

The time required for plants to reach reproductive maturity after fire was recorded for 108 species (Appendix 1). Since all species were not present at every site, and sites of one and three years-since-last-fire were not available, the exact number of years to reach reproductive maturity could not be assigned to most species. Many species, therefore, were given values of <2, <4>2, etc. A value of <4>2 means that the species was seen flowering in a four-year-old site, was not seen flowering in a two-year-old site and was not recorded in a three-year-old site, so therefore it flowers within three or four years after a fire. Most of the species (79%) required only two years at the most to begin flowering after fire regeneration.

There was no evidence that any species ceased flowering once a site reached maturity, i.e. greater than ten years-since-last-fire. The common belief that plants regenerating from seed have a longer juvenile period than sprouting species was unfounded in these results. Species reproducing from seed such as *Dryandra sessilis*, *D. kippistiana*, *Petrophile media* and *Leucopogon striatus*, for example, flowered on seedlings which were only two years old. Others, for example, *Hakea obliqua* and *Dryandra carlinioides*, however, required four years before they flowered. In these species a fire interval of three years could be disastrous and may lead to their local extinction. In heath vegetation of South Australia,

firing at intervals of less than five years was found likely to eliminate *Banksia ornata*, *Casuarina pusilla* and *Leptospermum myrsinoides*; species which take several years to reach reproductive maturity (Specht *et al.* 1958). In Victorian coastal heaths, *Leptospermum laevigatum* is killed by fire and requires four years before it flowers (Burrell 1968). Short fire intervals would be detrimental to the long term survival of such species.

In the Northern Sandplain region near Badgingarra, the impact of fire on the availability of flowers important to the bee keeping industry must also be considered. Species of the Epacridaceae, Fabaceae, Mimosaceae and Asteraceae are important pollen-producing species in the Northern Sandplain shrublands. During the winter months, *Leucopogon* species dominated the available flowers at nearly every site on both sand and laterite substrates which had a time-since-last-fire of four years or more. Since it only takes two years for seedlings of *Leucopogon striatus* to flower after a fire, it is unlikely that this species will be eliminated from an area by frequent burning. Another important pollen producer, *Acacia pulchella*, requires fire for establishment and flowering. Most plants of the heathland flower within four years after a fire. Although the dominant *Leucopogon* (winter) and Proteaceae (spring) species present in sites greater than four years since last fire did not dominate in recently burnt areas, the overall number of individuals and species in flower and density of flowering appeared as great in a two year old site as in a ten year old site. Whether the bees can utilise the flora of a recently burnt site though, is as yet untested. Given that honeybees can fly up to 11 km from their hive in search of favourable plants (A. Kessell, pers. comm.), it would take a large fire to render an apiary site completely unusable.

Species conservation management

Crown lands in the region must be managed to control the fuel build-up and a concomitant increase in the potential of uncontrollable fires starting within the shrub communities and spreading into the adjacent pasture and farmlands, thereby endangering human life and property (Bell and Loneragan, 1985). Other considerations, however, include the conservation of examples of this extremely rich flora and the maintenance of sufficient areas containing flowering species of importance to the honeybee.

Conservation of native flora everywhere is of growing concern since the rate of extinction is increasing rapidly as a result of man's activities (Leigh and Boden 1979). It has been estimated that, in tropical rainforests alone, at least one species is disappearing every day (Myers 1979). What this figure might be in the heathlands of Western Australia would be pure conjecture since many species here have yet to be described (Marchant and Keighery 1979).

The southwestern corner of Western Australia is characterized by a high degree of endemism. Marchant (1973) estimates that 68% of a listed 3 600 angiosperms in the South-West Botanical Province are restricted to this province. Marchant and Keighery (1979), in highlighting the lack of knowledge of the Western Australian flora, list over 2 000 species of vascular plants as being either poorly known or possibly rare or restricted to a small geographic area. With further taxonomic revision of local genera, as much as 25-30% of the south-west flora may be classified as rare (Marchant and Keighery 1979). Twenty-two of the 238 species recorded in the

study area can be classified as either rare, restricted or poorly known (Appendix 1). One species (*Eucalyptus pendens*) is classified as being rare and occurring in a restricted habitat. Only two small populations were observed in the lateritic sandplains of the southeastern section of the Badgingarra National Park. Seven species (*Cassytha pubescens*, *Dampiera lindleyi*, *Gastrolobium bidens*, *Hibbertia glaberrima*, *H. pilosa*, *Leucopogon crassifolia* and *Xanthorrhoea reflexa*) rank as poorly known, with only 2-5 specimens preserved in the Western Australian Herbarium. Six species (*Blancoa canescens*, *Conospermum nervosum*, *Daviesia epiphylla*, *Dryandra nana*, *D. tridentata* and *Hakea flabellifolia*) are classified as restricted to areas of less than 100 km diameter. Of these rare or poorly known species, six regenerate from seed and are therefore considered in most danger of elimination by fire, and, since a two year old site is probably incapable of carrying a fire, they are unlikely to be eliminated by this means alone. More data are needed on the flowering characteristics of *Gastrolobium bidens*, *Leucopogon crassifolius* and *Conospermum nervosum* to determine how many years are required after a fire before these species flower.

The remaining species collected from the study area which are not rare, restricted or poorly collected, all flower within five years after a fire. Most species were found to regenerate after fire by sprouting and are therefore not in danger of elimination from fire. Although the seed-regenerating species *Hakea obliqua* and *Dryandra carliniodes* require at least four years to flower following fire, neither are rare, nor restricted so are unlikely to be in danger of extinction from frequent fires.

Bee pasture management

The winter "hive-buildup" period in the Northern Sandplain heathlands is of major importance to the apicultural industry. During the early winter months, pollen collection from species of *Leucopogon* predominates. At least four years are required after a fire before *Leucopogon striatus*, the most abundant of the winter flowering *Leucopogon* spp., returns to flowering in abundance comparable to unburnt sites. During the first four years following fire, there are as many species flowering as in an unburnt site but since *L. striatus* is not flowering abundantly it is unknown whether recently burnt sites are capable of supporting an apiary site. Comparisons of the expected distances foraged by honeybees and the observations of fire scars visible in Landsat photographs of the northern sandplain indicate that fires of such magnitude to render an apiary site unusable have never been attained in years prior to 1984. Observations of flowering of old sites and especially important honeybee pollen species such as *Leucopogon striatus* indicates that no decline in flowering intensity appears with increasing site age. Therefore, there would appear to be no disadvantage to the apiarist in leaving a site unburned for many years and their claims for long-term fire protection may be based more on subjective visual assessment of apparent flowering intensity.

Fire hazard reduction

In monetary terms, fire is probably the cheapest management tool used in manipulating vegetation today. The introduction of prescribed burning in reducing the hazard of uncontrollable high-intensity fires has been widely used in forests, wilderness areas, nature reserves and national parks in the last decade or so in Australia (Gill 1977). The development of large

areas of the northern Sandplain heathlands for crop and agricultural uses since the 1960's places these at some risk from wildfires. The disastrous Beekeepers Reserve fire of January 1984 burned over 117 000 ha (Burking and Kessell 1984) and Northern Sandplain shrubland fires between February and May 1985 destroyed another 63 400 ha (Davies 1985). The losses in economic terms to the beekeeping industry could reach more than 5 million dollars over the next eight years (Davies 1985). The impact on conservation, tourism and the cut-flower and native seed industries is difficult to estimate but could also be considerable. For these reasons, alone, a policy on fire management for the Northern Sandplain shrublands is essential.

Before the establishment of farms and roads in the Badgingarra area, fires were a common occurrence on crown land during the late summer and autumn months. These fires appear to have been lit by lightning and usually burnt, uncontrolled, for one or two days before going out naturally (A. E. Eastwood, pers. comm.). Lightning is such a common occurrence during summer thunderstorms over this lateritic country that as soon as an area is capable of carrying a fire the chances of it remaining unburnt for any great length of time would seem to be low. The vegetation of sand and lateritic communities recovers to maximum cover in an average of eight years (Bell *et al.* 1984). More material capable of combustion, however, is available as the age of a kwongan stand increases up to at least 20 years. Therefore, the longer a "burnable" site is left unburnt, the more intense would be a fire and its potential destructive force.

The policy of "let nature take its own course" has operated advantageously in most large national parks in the past and is still in practice in many at present (Gill 1977). However, in areas of multiple land use, controlled fires under chosen conditions are more desirable to uncontrolled fires which may prove difficult to confine. Controlled burning of the Northern Sandplain area would necessarily involve rotational burning to eventually produce a mosaic of differing ages since-last-fire. Areas of more than 11 years-since-last-fire are however, becoming increasingly scarce. Efforts should therefore be made to create some areas which are protected from fire for as long as possible to allow for further research. These areas should not border on farmland in case of a wildfire. Ideally they should be enclosed by a wide buffer strip which is burnt more frequently and a fire break so that the chances of the area being burnt are reduced.

Any manipulation of the environment by man should attempt to closely reproduce the events of nature as much as possible. Applying this to fire management policies, it would be desirable to have controlled fires at a frequency close to that under more natural conditions. Policies of very frequent burning, or complete fire suppression should be avoided. Results from this study suggest the natural fire frequency in the Badgingarra area could be as low as between 8 and 15 years. A policy of controlled burning every 10 years in a mosaic pattern would: (1) be unlikely to cause any loss of species; (2) be unlikely to badly interfere with the apicultural industry unless the area burnt was very large; (3) would reduce the risk of uncontrolled wildfires; and (4) would closely simulate the actual fire pattern of the area under natural conditions.

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Appendix 1.

Vascular plant species of the northern sandplain honey bee pasture region. Annotated information where known includes edaphic preference, most preferred fire response mode, the juvenile period between fire and flower production and the dates of 1981 where flowering was recorded. Annotation codes: ¹Flowering mainly restricted to period 1 or 2 years following fire; ²Flowering restricted to period 2-4 years after fire; ³Flowers earlier in season in 2-4 year old sites; ⁴Species that are apparently rare and have a restricted geographic distribution (after Marchant and Keighery 1979); ⁵Species poorly known (after Marchant and Keighery 1979); ⁶Distribution restricted to an area with 100 km diameter (after Marchant and Keighery 1979); ⁷Distribution restricted to an area with 160 km diameter (after Marchant and Keighery 1979).

Species	Edaphic Preference	Fire Response	Juvenile Period	Flowering Period									
				4 29	5 28	6 10	7 7	8 5	9 1	9 29	11 20	12 19	
GYMNOSPERMAE													
Cupressaceae													
<i>Actinostrobus acuminatus</i> Parlat.	Generalist	Sprout									x	x	
ANGIOSPERMAE-MONOCOTYLEDONAE													
Cyperaceae													
<i>Causis diocea</i> R. Br.	Generalist	Sprout											
<i>Mesomelaena stygia</i> (R. Br.) Nees	Generalist	Sprout											
<i>Mesomelaena tetragona</i> (R. Br.) Benth.	Generalist	Sprout											
<i>Schoenus curvifolius</i> (R. Br.) Benth.	Generalist	Sprout											
Haemodoraceae													
<i>Anigozanthos humilis</i> Lindl.	Sand	Sprout	≤2						x	x			
<i>Blancoa canescens</i> (Lindl.) Baill.	Sand	Sprout	<2 ¹	x	x	x	x	x					
<i>Conostylis androstemma</i> Lindl.	Laterite	Sprout						x					
<i>Conostylis aurea</i> Lindl.	Generalist	Sprout	≤2							x	x		
<i>Conostylis filifolia</i> F. Muell.		Sprout	≤2					x	x				
<i>Conostylis teretifolia</i> J. W. Green	Generalist	Sprout											
<i>Haemodorum paniculatum</i> Lindl.		Sprout											
<i>Macropidia fuliginosa</i> Drum.	Laterite	Sprout											
<i>Phlebocarya ciliata</i> R. Br.		Sprout											
Iridaceae													
<i>Patersonia occidentalis</i> R. Br.	Generalist	Sprout	≤2								x		
Liliaceae													
<i>Burchardia umbellata</i> R. Br.	Generalist	Sprout	≤2							x			
<i>Johnsonia pubescens</i> Lindl.	Sand	Seed	≤2					x	x	x			
<i>Laxmannia grandiflora</i> Lindl.	Generalist	Seed						x	x				
<i>Laxmannia</i> sp. aff. <i>sessiliflora</i>		Seed											
<i>Thysanotus glaucus</i> Endl.	Sand	Seed									x	x	
<i>Thysanotus multiflorus</i> R. Br.	Sand	Seed	≤2								x	x	
Orchidaceae													
<i>Diuris longifolia</i> R. Br.	Laterite	Sprout	1				x						
<i>Glossodia brunonis</i> (Endl.) A. S. George	Laterite	Sprout								x			
<i>Prasophyllum parviflorum</i> Lindl.	Laterite	Sprout	≤2				x	x					
<i>Pterostylis nana</i> R. Br.		Sprout											
<i>Thelymitra</i> sp. aff. <i>variegata</i> Lindl.	Laterite	Sprout											
Poaceae													
<i>Neurachne alopecuroides</i> R. Br.		Sprout											
Restionaceae													
<i>Alexgeorgia arenicola</i> Carlquist	Generalist	Sprout											
<i>Anarthria laevis</i> R. Br.	Generalist	Sprout											
<i>Ecdeiocolea monostachya</i> F. Muell.	Generalist	Sprout											
<i>Hypolaena exsulca</i> R. Br.	Sand	Sprout											
<i>Lyginea barbata</i> R. Br.	Generalist	Sprout											
Xanthorrhoeaceae													
<i>Calectasia cyanea</i> R. Br.	Generalist	Sprout	<2				x	x	x	x	x	x	
<i>Dasypogon bromeliifolius</i> R. Br.	Sand	Sprout	<2 ¹						x	x			
<i>Kingia australis</i> R. Br.	Laterite	Sprout	<2 ¹										
<i>Xanthorrhoea reflexa</i> Herbert. ⁷	Laterite	Sprout	<2 ¹										
ANGIOSPERMAE-DICOTYLEDONAE													
Apiaceae													
<i>Xanthosia huegelii</i> (Benth.) Steud.	Sand												

Appendix 1—continued

Species	Edaphic Preference	Fire Response	Juvenile Period	Flowering Period											
				4 29	5 28	6 10	7 7	8 5	9 1	9 29	11 20	12 19			
Asteraceae															
<i>Angianthus tomentosus</i> Wendle.....	Generalist Sand	Seed	<2												
<i>Arctotheca calendula</i> (L.) Leogns.....		Seed	1												
<i>Helipterum cotula</i> (Benth.) D. C.....		Seed	1												
<i>Podotheca gnaphaloides</i> (Grah.) F. Muell.....		Sprout													
<i>Podotheca pygmaea</i> A. Gray.....		Seed	1												
<i>Ursinia anthemoides</i> (L.) Poir.....		Seed	1												
Caesalpiniaceae															
<i>Labichea punctata</i> Benth.....	Laterite	Sprout	<2								x				
Casuarinaceae															
<i>Allocasuarina humilis</i> Otto & Dietr.....	Generalist	Sprout			x	x	x								
<i>Allocasuarina microstachya</i> Miq.....	Laterite	Sprout													
Chloanthaceae															
<i>Lachnostachys verbascifolia</i> F. Muell.....	Sand	Sprout													
<i>Pityrodia bartlingii</i> (Lehm.) Benth.....	Sand	Sprout	<2										x		
Dilleniaceae															
<i>Hibbertia acerosa</i> (R. Br.) Benth.....	Sand	Sprout										x	x		
<i>Hibbertia aurea</i> Steud.....	Laterite	Sprout								x					
<i>Hibbertia crassifolia</i> (Turcz.) Benth.....	Generalist	Sprout	<2					x	x	x					
<i>Hibbertia glaberrima</i> F. Muell.....	Sand	Seed & Sprout	<2							x	x	x			
<i>Hibbertia huegii</i> (Endl.) F. Muell.....	Generalist	Sprout	<2						x	x	x				
<i>Hibbertia hypericoides</i> (DC.) Benth.....	Generalist	Sprout	<2					x	x	x	x				
<i>Hibbertia pilosa</i> Steud.....	Laterite	Sprout						x	x	x					
<i>Hibbertia racemosa</i> (Endl.) Gilg.....	Sand	Sprout													
Droseraceae															
<i>Drosera drummondii</i> Lehm.....	Laterite	Seed							x						
<i>Drosera erythrorhiza</i> Lindl.....		Sprout													
<i>Drosera heterophylla</i> Lindl.....	Generalist	Sprout	<2					x	x						
<i>Drosera macrantha</i> Endl.....	Sand	Sprout	<2								x				
<i>Drosera menziesii</i> R. Br.....		Sprout													
<i>Drosera paleacea</i> DC.....		Sprout													
<i>Drosera pallida</i> Lindl.....		Seed													
Epacridaceae															
<i>Andersonia heterophylla</i> Sond.....	Sand	Seed & Sprout	≈4				x	x	x						
<i>Andersonia lehmanniana</i> Sond.....	Generalist	Sprout	≈4												
<i>Astroloma microdonta</i> (F. Muell.) Benth.....	Laterite	Seed	≈4			x	x	x	x						
<i>Astroloma pallidum</i> R. Br.....	Laterite	Seed	≈4			x	x	x	x	x	x				
<i>Astroloma serratifolium</i> (DC.) Druce.....	Laterite	Sprout	≈2			x	x	x							
<i>Astroloma stomarrhena</i> Sond.....	Generalist	Sprout	≈2					x							
<i>Astroloma xerophyllum</i> (DC.) Sond.....	Generalist	Sprout	≈2					x	x	x					
<i>Conostephium pendulum</i> Benth.....	Sand	Seed	≈4						x	x					
<i>Leucopogon striatus</i>	Sand	Sprout	≈5						x						
<i>Leucopogon conostephioides</i> DC.....	Generalist	Sprout & Seed	≈2	x	x	x	x	x	x	x	x				
<i>Leucopogon crassiflorus</i> F. Muell. ^s	Generalist	Seed	≈5					x	x						
<i>Leucopogon cryptanthus</i> Benth.....	Sand		≈5						x	x	x				
<i>Lysinema ciliatum</i> R. Br.....	Generalist											x	x		
<i>Lysinema ciliatum</i> R. Br.....	Sand	Seed	≈4					x	x	x					
Euphorbiaceae															
<i>Monotaxis grandiflora</i> Endl.....															
Goodeniaceae															
<i>Dampiera juncea</i> Benth.....	Generalist														
<i>Dampiera lindleyi</i> De Vriesse ^s	Laterite	Sprout									x	x	x		
<i>Dampiera spicigera</i> Benth.....	Sand	Sprout													
<i>Dampiera stenostachya</i> E. Pritzel.....											x	x			
<i>Lechenaultia biloba</i> Lindl.....	Laterite	Sprout	≈2												
<i>Lechenaultia floribunda</i> Benth.....		Seed									x				
<i>Lechenaultia formosa</i> R. Br.....	Sand														
<i>Scaevola canescens</i> Benth.....	Sand	Sprout													
<i>Scaevola glandulifera</i> DC.....								x	x						
<i>Scaevola paludosa</i> R. Br.....															
<i>Scaevola paludosa</i> R. Br.....	Sand	Sprout													
<i>Velleia trinervis</i> Labill.....	Sand	Seed													
<i>Verreauxia villosa</i> E. Pritzel.....	Sand	Seed	2												
<i>Verreauxia villosa</i> E. Pritzel.....															
Haloragaceae															
<i>Glischrocaryon aureum</i> var. <i>aureum</i> (Lindl.) Orch.....											x				
Lauraceae															
<i>Cassytha pubescens</i> R. Br. ^s	Sand	Seed													
Lamiaceae															
<i>Hemianandra pungens</i> R. Br.....	Sand	Sprout													
<i>Hemianandra pungens</i> R. Br.....															
Lobeliaceae															
<i>Lobelia gibbosa</i> Labill.....															

Appendix 1—continued

Species	Edaphic Preference	Fire Response	Juvenile Period	Flowering Period									
				4	5	6	7	8	9	9	11	12	
				29	28	10	7	5	1	29	20	19	
Loganiaceae													
<i>Logania spermacoea</i> F. Muell.	Generalist										x	x	
Loranthaceae													
<i>Nuytsia floribunda</i> (Labill.) R. Br.	Sand	Sprout											
Malvaceae													
<i>Plagianthus monoica</i> Ewart													
Mimosaceae													
<i>Acacia auronitens</i> Lindl.		Sprout & Seed											
<i>Acacia cedroides</i> Benth.	Laterite		≤2				x	x					
<i>Acacia lasiocarpa</i> Benth.	Laterite	Seed											
<i>Acacia pulchella</i> R. Br.	Generalist	Seed	≤5>2					x	x				
<i>Acacia spinosissima</i> Benth.	Sand												
<i>Acacia stenoptera</i> Benth.		Sprout	≤5>2		x	x	x						
<i>Acacia teretifolia</i> Benth.	Laterite							x					
Myrtaceae													
<i>Baeckea camphorosmae</i> Endl.	Generalist									x			
<i>Baeckea crispiflora</i> F. Muell.	Laterite												
<i>Baeckea grandiflora</i> F. Muell.	Laterite	Sprout	<4>2							x	x	x	
<i>Beaufortia bracteosa</i> Diels.		Seed											
<i>Beaufortia elegans</i> Schau.	Sand	Seed	≤2								x	x	
<i>Beaufortia eriocephala</i> W. V. Fitzg.	Laterite	Sprout & Seed	<2								x	x	
<i>Beaufortia squarrosa</i> Schau.		Seed	<2								x	x	
<i>Calothamnus sanguineus</i> Labill.	Generalist	Sprout	<4	x	x	x	x	x	x	x	x	x	
<i>Calothamnus torulosus</i> Schau.	Laterite	Sprout	≤5>2							x			
<i>Calytrix brachyphylla</i> Turcz.	Sand	Sprout	<2										
<i>Calytrix flavescens</i> A. Cunn.	Sand										x	x	
<i>Calytrix muricata</i> F. Muell.	Sand												
<i>Conothamnus trinervis</i> Lindl.	Generalist	Sprout	≤2							x			
<i>Darwinia speciosa</i> (Meissn.) Benth.	Generalist	Sprout											
<i>Eremaea beaufortoides</i> Benth.	Generalist	Sprout	≤2 ²							x	x	x	
<i>Eremaea fimbriata</i> Lindl.	Generalist	Seed											
<i>Eucalyptus macrocarpa</i> Hook.	Sand	Sprout											
<i>Eucalyptus pendens</i> Brooker ⁷	Laterite	Sprout											
<i>Eucalyptus todiana</i> F. Muell.	Sand	Sprout											
<i>Hypocalymma xanthopetalum</i> F. Muell.	Generalist	Sprout	≤2				x	x	x				
<i>Leptospermum spinescens</i> Endl.	Generalist	Sprout									x		
<i>Melaleuca depressa</i> Diels.	Generalist	Sprout									x	x	
<i>Melaleuca scabra</i> R. Br.	Generalist	Sprout								x	x	x	
<i>Melaleuca trichophylla</i> Lindl.	Laterite	Sprout	<4>2							x	x		
<i>Pileanthus filifolius</i> Meissn.	Generalist		<4								x	x	
<i>Verticordia densiflora</i> Lindl.	Generalist										x		
<i>Verticordia grandiflora</i> Endl.	Generalist	Seed	<4							x			
<i>Verticordia grandis</i> Drum. ⁷	Sand	Sprout	<2	x	x	x					x	x	
<i>Verticordia spicata</i> F. Muell.													
<i>Verticordia ovalifolia</i> Meissn.											x	x	
Papilionaceae													
<i>Daviesia aphylla</i> (F. Muell.) Benth.	Laterite	Sprout	≤2							x			
<i>Daviesia daphnoides</i> Meissn.	Laterite	Sprout		x	x	x	x						
<i>Daviesia divaricata</i> Benth.	Sand	Sprout	≤2					x					
<i>Daviesia epiphylla</i> Meissn. ⁶	Laterite	Sprout											
<i>Daviesia juncea</i> Sm.	Laterite	Sprout								x			
<i>Daviesia madiflora</i> Meissn.	Generalist	Sprout	≤2				x	x					
<i>Daviesia pectinata</i> Lindl.	Generalist	Sprout	≤2				x	x					
<i>Daviesia pedunculata</i> Benth.	Generalist	Sprout	<2							x			
<i>Daviesia preissii</i> Meissn.	Generalist	Sprout		x	x								
<i>Daviesia quadrilobata</i> Benth.	Sand	Seed	≤2				x	x	x				
<i>Daviesia striata</i> Turcz.	Laterite	Sprout		x									
<i>Gastrolobium huius</i> Meissn. ⁵	Laterite	Seed						x	x				
<i>Gastrolobium ilicifolium</i> Meissn.	Laterite												
<i>Gastrolobium obovatum</i> Benth.	Laterite	Sprout	≤5					x					
<i>Gastrolobium oxyloboides</i> Benth.	Laterite	Sprout											
<i>Gastrolobium spinosum</i> Benth.	Laterite	Seed									x	x	
<i>Gastrolobium knightianum</i> Lindl.	Laterite	Sprout											
<i>Hovea stricta</i> Meissn. ⁷	Generalist	Sprout	≤2		3	x	x	x					
<i>Isotropis cuneifolia</i> (Sm.) Domin.	Generalist	Sprout	≤2 ²								x	x	
<i>Jacksonia floribunda</i> Meissn.	Sand	Seed & Sprout	≤2							x	x		
<i>Jacksonia restioides</i> Hueg.	Generalist												
<i>Jacksonia sternbergiana</i> R. Br.	Laterite	Seed											
<i>Kennedia prostrata</i> R. Br.	Laterite	Seed											
<i>Oxylobium capitatum</i> Benth.	Laterite												
<i>Sphaerolobium macranthum</i> Meissn.	Laterite									x			
Phytolaccaceae													
<i>Gyrostemon ramulosus</i> Desf.	Sand	Seed	<2									x	
<i>Tersonia brevipes</i> Moq.	Sand	Seed	<2						x	x	x	x	
Pittosporaceae													
<i>Billardiera bicolor</i> (Putterl.) E. M. Bennett	Laterite												

Appendix 1—continued

Species	Edaphic Preference	Fire Response	Juvenile Period	Flowering Period											
				4 29	5 28	6 10	7 7	8 5	9 1	9 29	11 20	12 19			
Polygalaceae															
<i>Comesperma calymega</i> Labill.	Generalist	Sprout	≤2								x	x	x		
Proteaceae															
<i>Adenanthos eynorum</i> Dies.	Sand	Seed										x			
<i>Banksia attenuata</i> Meissn.	Sand	Sprout & Seed	<2									x	x		
<i>Banksia candolleana</i> Meissn. ⁷	Sand	Sprout	≤4>2	x	x	x	x	x							
<i>Banksia menziesii</i> R. Br.	Laterite	Sprout	≤2	x	x	x	x	x	x						
<i>Banksia prostrata</i> R. Br.	Laterite	Sprout	≤2									x			
<i>Banksia sphaerocarpa</i> R. Br.	Generalist	Seed & Sprout											x		
<i>Banksia</i> sp. aff. <i>sphaerocarpa</i> R. Br.	Generalist	Seed & Sprout	≤2		x	x	x						x		
<i>Conospermum acerosum</i> Lindl.	Sand	Sprout									x				
<i>Conospermum incurvum</i> Lindl.	Sand	Sprout	<5									x			
<i>Conospermum nervosum</i> Meissn. ⁶	Laterite	Seed													
<i>Conospermum stoechadis</i> Endl.	Sand	Sprout	<2								x				
<i>Conospermum triplinervium</i> R. Br.	Sand	Sprout	<2	x	x	x						x	x		
<i>Dryandra bipinnatifida</i> R. Br.	Laterite	Sprout & Seed													
<i>Dryandra carlinoides</i> Meissn.	Generalist	Seed	≤4>2									x			
<i>Dryandra kippistiana</i> Meissn.	Laterite	Seed	<2						x	x					
<i>Dryandra nana</i> Meissn. ⁵	Generalist	Sprout	<2									x			
<i>Dryandra nivea</i> R. Br.	Generalist	Sprout										x			
<i>Dryandra sessilis</i> (R. Br.) Druce.	Laterite	Seed	≤2									x			
<i>Dryandra shuttleworthiana</i> Meissn.	Generalist	Sprout													
<i>Dryandra tridentata</i> Meissn. ⁶	Sand	Sprout	<2									x			
<i>Grevillea ptilulifera</i> (Lindl.) C. A. Gardn.	Generalist	Sprout					x	x	x						
<i>Grevillea shuttleworthiana</i> Meissn.	Sand	Sprout										x			
<i>Grevillea synapheae</i> R. Br.	Laterite	Seed	≤2					x	x	x					
<i>Hakea auriculata</i> Meissn.	Laterite	Sprout	≤2						x	x	x				
<i>Hakea conchifolia</i> Hook.	Laterite	Sprout	<2					x	x	x					
<i>Hakea corymbosa</i> R. Br.	Generalist	Sprout				x	x	x	x						
<i>Hakea costata</i> Meissn.	Sand	Seed	≤6									x			
<i>Hakea flabellifolia</i> Meissn. ⁶	Generalist	Sprout													
<i>Hakea incrassata</i> R. Br.	Laterite	Sprout	≤2					x							
<i>Hakea lissocarpa</i> R. Br.	Generalist	Sprout		x	x	x	x								
<i>Hakea obliqua</i> R. Br.	Sand	Seed	≤4									x			
<i>Hakea prostrata</i> R. Br.	Sand	Sprout									x				
<i>Hakea ruscifolia</i> Lahill.	Sand														
<i>Hakea sulcata</i> var. <i>scoparia</i> R. Br.	Laterite	Seed									x				
<i>Hakea undulata</i> R. Br.															
<i>Isopogon asper</i> R. Br.	Laterite		<2							x					
<i>Isopogon linearis</i> Meissn. ⁷		Sprout	≤4>2							x					
<i>Isopogon teretifolius</i> R. Br.															
<i>Lambertia multiflora</i> Lindl.	Generalist	Sprout	≤2							x	x	x			
<i>Persoonia dillwynioides</i> Meissn.	Laterite	Sprout	≤4									x	x		
<i>Petrophile inconspicua</i> Meissn.	Generalist	Sprout & Seed						x							
<i>Petrophile linearis</i> R. Br.	Sand	Sprout	≤2									x			
<i>Petrophile macrostachya</i> R. Br.	Generalist	Sprout	≤4									x			
<i>Petrophile media</i> R. Br.	Generalist	Seed	≤2							x	x				
<i>Petrophile serrariae</i> R. Br.															
<i>Petrophile striata</i> R. Br.	Generalist	Sprout & Seed										x			
<i>Stirlingia latifolia</i> (R. Br.) Steud.	Sand	Sprout	≤2							x					
<i>Stirlingia simplex</i> Lindl.		Sprout													
<i>Strangea cyanchioides</i> F. Muell. ⁷	Sand	Sprout													
<i>Synaphaea petiolaris</i> R. Br.	Laterite	Sprout									x	x			
<i>Synaphaea polymorpha</i> R. Br.	Generalist	Sprout & Seed	≤2								x	x			
Rhamnaceae															
<i>Cryptandra arbutiflora</i> Fenzl.															
<i>Cryptandra pungens</i> Steud.															
<i>Spyridium tridentatum</i> (Steud.) Benth.	Laterite				x	x	x	x							
<i>Spyridium</i> sp. aff. <i>tridentatum</i> (Steud.) Benth.	Generalist	Seed	≤2						x	x	x				
<i>Trymalium ledifolium</i> Fenzl.	Laterite														
Rutaceae															
<i>Boronia ramosa</i> (Lindl.) Benth.	Laterite														
<i>Eriostemon spicatus</i> A. Rich.	Generalist	Sprout	≤2									x			
Stackhousiaceae															
<i>Stackhousia brunonis</i> Benth.	Laterite	Sprout & Seed	≤2									x			
<i>Stackhousia pubescens</i> A. Rich.	Sand														
Sterculiaceae															
<i>Commersonia pulchella</i> Turcz.	Sand														
<i>Lasiopetalum drummondii</i> Benth. ⁷	Generalist	Sprout	≤2												
<i>Lasiopetalum</i> sp.															
<i>Thomasia grandiflora</i> Lindl.	Laterite	Sprout	≤2						x	x	x				

Appendix 1—continued

Species	Edaphic Preference	Fire Response	Juvenile Period	Flowering Period									
				4 29	5 28	6 10	7 7	8 5	9 1	9 29	11 20	12 19	
Stylideaceae													
<i>Stylidium adpressum</i> Benth.		Seed											
<i>Stylidium leptophyllum</i> DC.		Seed											
<i>Stylidium piliferum</i> ssp. <i>minor</i> (Mildbr.) Carlq.	Laterite	Seed	≤ 2 ²								x		
<i>Stylidium repens</i> R. Br.	Generalist	Seed	≤ 2			x	x	x					
Thymeleaceae													
<i>Pimelea angustifolia</i> R. Br.	Generalist	Sprout											
<i>Pimelea floribunda</i> Meissn.		Seed											
<i>Pimelea imbricata</i> R. Br.													
<i>Pimelea suaveolens</i> (Endl.) Meissn.	Laterite	Seed	≤ 2 ²										
<i>Pimelea sulphurea</i> Meissn.		Sprout & Seed									x		
Tremandraceae													
<i>Tetratheca confertifolia</i> Steetz.	Laterite										x	x	
Violaceae													
<i>Hybanthus calycinus</i> (Steud.) F. Muell													
<i>Hybanthus floribundus</i> (Walp.) F. Muell	Laterite		≤ 2					x	x				

Northern Sandplain Kwongan: community biomass and selected species response to fire

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Abstract

The mixed, taxonomically diverse shrublands of the Northern Sandplains near Badgingarra, Western Australia recover rapidly following fire and by seven years, above ground biomass has reached a maximum of about 16-18 t ha⁻¹. Such rapid build up of biomass is typical of fire-prone communities of kwongan dominated by long-lived autoregenerating species. Sampling from a series of deep sand sites of known fire history provided material for case studies of biomass recovery and development of polycarpic fire ephemeral (*Tersonia brevipes* Moq. in DC.), four obligatory reseeding species (*Leucopogon conostephioides* DC., *Petrophile media* R. Br., *Beaufortia elegans* Schauer, and *Hakea obliqua* R. Br.), a species normally exhibiting both seed- and resprouting-regeneration (*Jacksonia floribunda* Endl.), and two long-lived resprouting species never recorded at the sites as currently regenerating from seed (*Hibbertia hypericoides* (DC.) Benth. and *Hypocalymma xanthopetalum* F. Muell.). Very great differences were observed between representatives of each fire response category in growth rates and shapes of developing shoot canopies of the species. Community biomass was directly correlated with foliage projective cover allowing an easily obtained value to estimate fire fuels. The implications of the data are considered in relation to the prediction of fuel loads and design of controlled burning regimes for the region.

Introduction

Upland regions in the Irwin District of the kwongan of the South-West Botanical province (Beard 1980) are dominated by shrublands of highly uniform visual appearance but of great floristic richness and diversity (Lamont *et al.* 1984, Bell and Loneragan 1985). The mediterranean weather pattern of the region, by providing cool wet winters and long dry summers, promotes a rapid accumulation of above ground biomass between successive fires. These conditions, compounded with the tendency for certain plant species to be highly flammable in living or dead state (Pompe and Vines 1966), present serious summer fire control problems for land managers in the region, especially where fire-prone natural plant communities are intermixed with farmland committed to arable crops or pasture.

Fire management in the Northern Sandplains is aimed at fulfilling two major criteria. First and foremost farmers and pastoralists must be protected from wildfires emanating from adjacent native vegetation. Secondly, sufficient areas of native plant communities must be maintained for conservation purposes, while still serving the needs of a commercial apiculture industry, the wildflower seed and cut-flower trades, and tourism (Bell *et al.* 1984). These areas of native vegetation must in turn be protected from fires originating from roadsides or burning operations in adjacent farmland.

Techniques for estimating fuel loads in the shrublands of the Northern Sandplain have recently been developed (Schneider and Bell 1985), and certain general characteristics of the response to fire by vegetation in the region have been considered in relation to apiculture (van der Moczal *et al.* 1987). The vegetation generally increases to a near maximum value of 70% foliage projective cover within 7-10 years (Bell *et al.* 1984), rates of recovery being more rapid in plant communities of the lateritic peneplain surfaces than on adjacent quartzitic sands. The floristic composition of these two edaphically-distinct substrata is also quite different, so differing recovery profiles might relate as much to the species present as to contrasting soil types (Bell and Loneragan 1985).

The first objective of this study was to document community foliage canopy cover and biomass changes occurring after fire in the vegetation of a series of deep sand sites, using a combination of projective cover density measurements and direct assessments of dead and living plant material harvested from randomly selected quadrats within a series of sites of known fire history. A second objective was to examine in detail patterns of biomass recovery in a number of common species typifying the major classes of fire response (see Bell *et al.* 1984) shown by flora of the study area. The data obtained are discussed in relation to the development of rational and effective fire management policies for the region.

Methods

The study area was centred around Badgingarra (30°23'S, 115°30'E), approximately 200 km north of Perth, Western Australia. Individual sites extended from the Badgingarra National Park (30°20'S, 115°25'E) northwards to the region of Jurien Road (30°14'S, 115°16'E). They were selected on the basis of records of the Western Australian Bush Fires Board to represent stands burned 5 and 9 months, and 2, 3, 4, 5, 6, 7, 8, 11, 12 and 17 years prior to sampling in March 1982. The study sites lay over deep quartzite, nutrient-poor sands, analytical data for which have been recently published (Pate *et al.* 1985).

Records of community above-ground biomass were determined by collecting all living and dead plant material from ten randomly selected 1 m² quadrat samples at each site. The samples from each quadrat were weighed individually in the field using spring balances, and weighed subsamples of bulked material from each site taken back to the laboratory for oven drying (65°C), to enable field biomass fresh weight data to be converted to dry matter. Each quadrat was assayed for foliage projection cover before its biomass was collected, so that relationships between biomass and cover and between biomass and age since last fire could be determined by linear regression analysis.

A detailed analysis of developing canopy structure was made for 8 common shrubby species (Table 1) which collectively included all major categories of response to fire represented in the community. Twenty individuals of a species were collected from all sites at which that species was present. The above ground parts of each individual plant were air dried in intact state and then partitioned horizontally into a series of 10 cm segments (except for the large species *Hakea obliqua* with 20 cm increments). Each stratum of the shoot was then measured for foliage diameter and dry weight. Combining data for each sample of 20 plants, shrub structure profiles were then constructed depicting mean canopy shape and weight distribution for each species for the range of ages since last burn (Gibberto *et al.* 1977).

Results and discussion

Increase in community biomass following fire

Canopy cover and above-ground biomass in the study area increase rapidly in the first 7 years following fire, thereafter tending to remain at levels of approximately 16–18 t ha⁻¹ (Fig. 1). This period of rapid increase in biomass correlates with the main flush of regeneration of woody shrubs establishing from fire-resistant underground root stocks. A study of 152 species from sandy habitats in the Badgingarra-Jurien region has indicated that 66% resprouted in such manner following fire, and that at least a similar proportion of biomass of a site was likely to consist of these resprouter species (Bell *et al.* 1984). Other studies on sandy sites from the region, and of the floras of neighbouring lateritic sites have shown even higher proportions of resprouting species (Bell and Loneragan 1985, van der Moezel *et al.* 1987).

The plateau of biomass at approximately 16–18 t ha⁻¹ places the Northern Sandplain kwongan at the low end of values for above-ground biomass recorded for mediterranean-climate shrubland ecosystems in California, France and the eastern Australian states (see Gray and Schlesinger 1981, Bell *et al.* 1984). Biomass achievements of Northern Sandplain shrublands are,

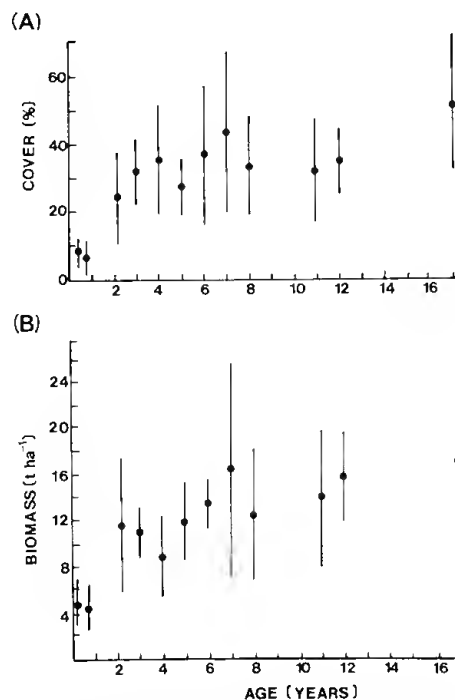


Figure 1.—Foliage projective cover percentage (A) and total above ground biomass (litter plus above-ground plant material) (B) of deep sand shrubland sites in the Northern Sandplain region between Badgingarra and Jurien, Western Australia.

however, more than double those reported for the open matorral of Chile (Mooney *et al.* 1977), and lie within the range of 11–26 t ha⁻¹ reported for mature shrub-dominated communities in southwest Cape Province, South Africa (Kruger 1977). Elsewhere in the kwongan of Western Australia, biomass values for closed shrub communities on calcareous sands at Two Peoples Bay near Albany were reported to have reached near-maximum biomass at 16 t ha⁻¹ after 9 years regrowth (Bell *et al.* 1984); a site on deep sands south of Eneabba carried 7 t ha⁻¹ after 9 years (Hopkins and Hnatiuk 1981), and a mature shrub-dominated stand of unknown age on depauperate grey sands at Tutanning Nature Reserve showed 13 t ha⁻¹ (Brown and Hopkins 1983). As mentioned above, relatively early achievement of a plateau in biomass with age in kwongan is probably related primarily to the large (Fig. 1B) proportional contribution of sprouters to the ecosystem, but it might equally reflect a limited overall carrying capacity in the dry, nutrient-poor sites typical of this class of vegetation.

Cover to biomass relationships

Analyses of data from all study sites showed that foliage projective cover percentages were directly related to biomass according to the following regression equation (biomass (t ha⁻¹) = 2.99 + 0.25 cover (%), df = 115, r = 0.85, p < 0.01). An essentially similar pattern of biomass recovery following fire is reported for South African fynbos communities (Kruger 1977), although the perennial herbaceous component of these communities is greater than kwongan.

Other published data on cover density have provided estimates of vegetation recovery following fire in a number of mediterranean-climate vegetation types. For coastal heaths at Dark Island, South Australia, cover percentages increase steadily to a maximum of approximately 70% after 10 years since burning, and

remain fairly constant for the next 15 years (Specht *et al.* 1958). Cover values following fires in the chaparral of southern California, however, show two peak periods, the first after 2-5 years coincide with dominance by annuals, herbaceous perennials and short-lived subshrubs, the second peak, after 8-17 years, with the resurgence of larger woody shrubs typical of the climax mature vegetation of the region (Horton and Knaebel 1955, Keeley and Keeley 1981). According to Specht *et al.* (1985) cover values for fire-prone vegetation possessing a herbaceous phase in its pyric succession are generally not well correlated with biomass, due to the much greater weight to cover ratio of later stage samples (Specht *et al.* 1985).

The rapid regrowth of the Northern Sandplain shrublands means that stands achieve a capacity to support a fire very soon after the previous fire. Indeed, instances of fires burning through regions carrying only a three-year-old fuel load have been reported for the Beekkeepers Reserve north of Jurien, albeit only under conditions of exceptionally intense late summer temperatures ($>40^{\circ}\text{C}$) involving low humidities ($<15\%$), high winds ($>40\text{ km hr}^{-1}$) and dry fuel conditions (Burking and Kessell 1984). It is apparent, however, that on average, stands of age 2-6 years will have considerable less biomass than older counterparts and would be accordingly less prone to wildfires. Prescribed burning on a rotation of five to seven years, or even less, would therefore appear to be an eminently sensible means of reducing fuel loads to less dangerous proportions. However, this advantage must be weighed against potential problems in conservation of individual species, especially rare or restricted fire sensitive species which normally take a number of years after germination before commencing to flower and set seed (see Hopper and Muir 1984). This will constitute a particularly serious problem where the species in question retain their seed load in the plant canopy rather than in the soil (Table 1).

Table 1

Characteristics of species selected for detailed study on recovery after fire.

Species	Family	Regeneration Mode	Seed Store
<i>Leucopogon conostephioides</i> ...	Epacridaceae	Obligate seed regenerator	Soil
<i>Hakea obliqua</i>	Proteaceae	Obligate seed regenerator	Plant
<i>Beaufortia elegans</i>	Myrtaceae	Obligate seed regenerator	Plant
<i>Tersonia brevipes</i>	Phytolaceae	Obligate seed regenerator	Soil
<i>Petrophile media</i>	Proteaceae	Obligate seed regenerator	Plant
<i>Hibbertia hypericoides</i>	Dilleniaceae	Resprouter	Soil
<i>Jacksonia floribunda</i>	Papilionaceae	Both a resprouter and reseed	Soil
<i>Hypocalymma xanthopetalum</i>	Myrtaceae	Resprouter	Soil

Growth and developing canopy characteristics of selected species

(a) Polycarpic fire ephemerals

Monocarpic and polycarpic fire ephemerals are relatively sparse in the Northern Sandplain in terms of number of species and relative biomass (Pate *et al.* 1985) in comparison with the highly prolific post-fire herb flora of Californian chaparral (Muller *et al.* 1968, Keeley and Keeley 1981). The species *Tersonia brevipes* is a typical short-lived polycarpic perennial of kwongan in showing fire-obligate germination, extremely fast early

growth rates, early maturity, high reproductive effort in proportion to vegetative biomass, and a relatively short life span (see Pate *et al.* 1985). Fast early growth of these successional species is generally held to promote an immediate conservation of nutrients following disturbance such as fire, and thus minimize leaching losses of nutrients in such circumstances (Marks and Bormann 1972, Likens *et al.* 1978, Foster *et al.* 1980, Nilsen and Schlesinger 1981).

Initial growth in *Tersonia brevipes* (Fig. 2a) was predominantly in a vertical direction though formation of a short lived leafy shoot, but a semi-woody creeping habit is then quickly attained through subsequent development of a number of basal axillary shoots. By four years the radiating stems of plants of the species may encompass an area up to 240 cm in diameter with all biomass restricted essentially to within 10 cm of ground level. By 4 years mean plant weight had reached 220 g, but by 5 years virtually all plants had senesced and died within the area (see also Pate *et al.* 1985).

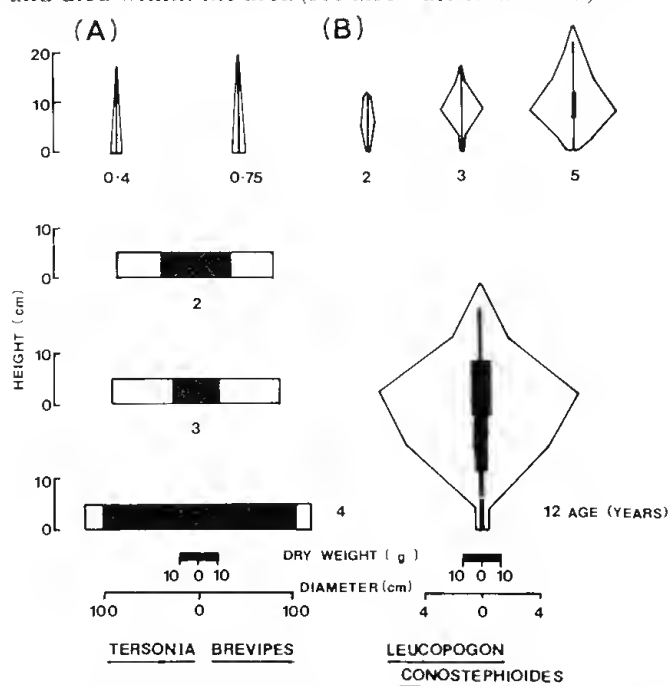


Figure 2.—Mean shrub dimensions of the short-lived fire ephemeral, *Tersonia brevipes*, following fire in the Northern Sandplain shrublands (A). Histogram of dry weight for 10 cm increments of radial distribution from the root system.

Mean shrub dimensions of obligatory reseed species, *Leucopogon conostephioides*, following fire (B). Data includes height, 10 cm increment diameter and dry weight distribution and total dry weight.

(b) Obligatory re-seeding species

Patterns of regrowth following fire were essentially the same in the two seeder species *Leucopogon conostephioides* (Fig. 2b), and *Beaufortia elegans* (Fig. 3a). Over the first two years each species grew mostly in a vertical fashion, but thereafter increasingly in diameter as well as in height. In *Leucopogon conostephioides*, mean plant above ground dry weight increased from 0.20 g plant⁻¹ at two years to 0.36 g after 3 years, 2.7 g after 5 years and 9.6 g plant⁻¹ after nine years growth (Fig. 2b). Mean heights of the 2-, 3-, 5- and 12-year plants were 11, 17, 23 and 44 cm, respectively. As plants aged, biomass tended to be distributed disproportionately toward the upper part of the stem, giving a decidedly "top heavy" plant.

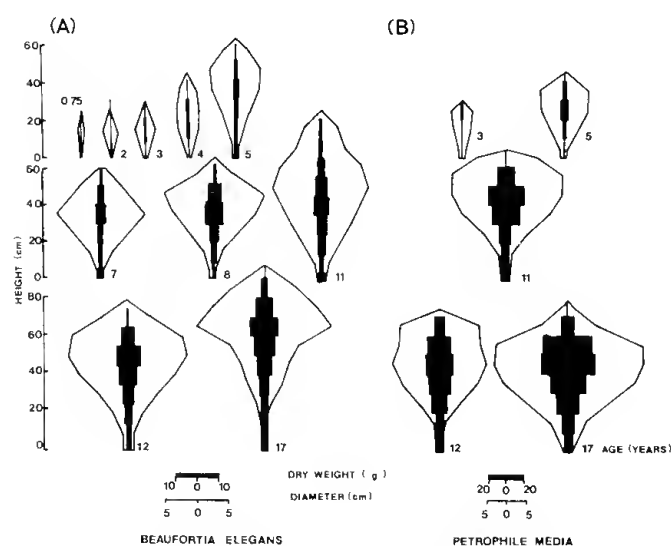


Figure 3.—Mean shrub dimensions of obligatory reseeding species, *Beaufortia elegans* (A), and *Petrophile media* (B) following fire in the Northern Sandplain shrublands.

Beaufortia elegans seedlings were generally larger than those of comparably-aged *Leucopogon conostephioides*. Plants of *B. elegans* growing in a 17-year old stand were nearly 100 cm tall and weighed more than 75 g (Fig. 3a). In these old plants the stratum between 60 and 70 cm above soil level contained the greatest amount of biomass.

Petrophile media, another obligatory reseeding species, was unfortunately encountered only at sites within the age range 3-17 years. When mature, this species showed similar "top heavy" biomass distribution profiles to those of *Beaufortia elegans*, although above ground parts of *P. media* plants were generally more than twice as large and heavy as *B. elegans* (Fig. 3b).

The largest obligatory reseeding species encountered in the deep sand communities of the study region was *Hakea obliqua* (Fig. 4). In areas estimated to be 17 years old since the last fire, plants had a mean height of 2.7 m and a mean above ground dry weight of 1.44 kg. The distribution of this biomass with height was more uniform in this species compared with the previous three examples, as readily apparent from the generally spindly profile of the species in the field.

Table 2

Linear regression equations and statistics for the relationship of mean plant height and age for four obligatory reseeding species of the Northern Sandplain shrublands.

Regression Equation	d.f.	v	p
Age (yr) = $-1.32 + 0.41$ <i>Leucopogon conostephioides</i> height (cm).....	50	99	< 0.01
Age (yr) = $-2.89 + 0.21$ <i>Beaufortia elegans</i> height (cm).....	80	94	< 0.01
Age (yr) = $-4.28 + 0.29$ <i>Petrophile media</i> height (cm).....	40	96	< 0.01
Age (yr) = $-2.90 + 0.07$ <i>Hakea obliqua</i> height (cm).....	90	99	< 0.01

Highly significant linear regressions between height and age were found for each of these four obligatory seed-regenerating species (Table 2). This relationship has already been suggested as a useful means for predicting age of sites for when fire records are not available (Bell 1985). We would now further suggest that, using such regression equations, and data on mean heights of a range of seeder species, one would have a simple method

for estimating stand age at a site for which fire records were not available. Following this, using the age-biomass data of Fig. 1., predictions could be made of fuel loads in the region, and thus determine whether or not a prescribed burn were both feasible and desirable.

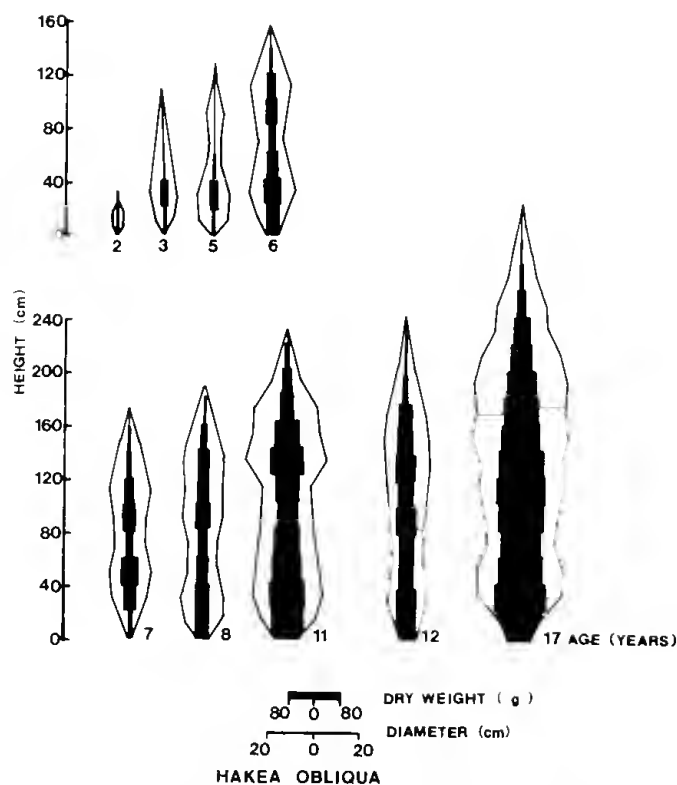


Figure 4.—Mean shrub dimensions of the obligatory reseeding species *Hakea obliqua* following fire in the Northern Sandplain shrublands.

(c) Resprouting species also regenerating freely from seed

Species which possess the ability both to resprout, and to establish abundant seedlings following fire may be considered to have distinct advantages over species exhibiting only one or other of these regeneration strategies. For instance, Keeley (1977) noted that the most abundant chaparral species in California, *Adenostoma fasciculatum*, reproduces following fire both by resprouting and from germinating seed, as do a number of successful species of the Californian coastal sage vegetation (Malanson and O'Leary 1982).

In the Northern Sandplain of Western Australia, *Jacksonia floribunda*, constitutes a common species possessing the above mentioned abilities (Bell *et al.* 1984). By being able to distinguish between unscarred seedlings established following the last fire and fire-scarred resprouting individuals which had clearly survived at least one fire at the site, it was possible to compare growth patterns and morphologies of virgin seedlings and previously established survivors. Seedlings of *Jacksonia floribunda* were then found to produce above-ground biomass at very slow rates, yielding after eight years, heights of approximately 40 cm and above ground dry weights of only 2.7 g dry weight (Fig. 5a). By comparison resprouting individuals in the same 8-year study site averaged nearly 80 cm in height and carried above-ground biomass averaging of 79 g dry weight (Fig. 5b).

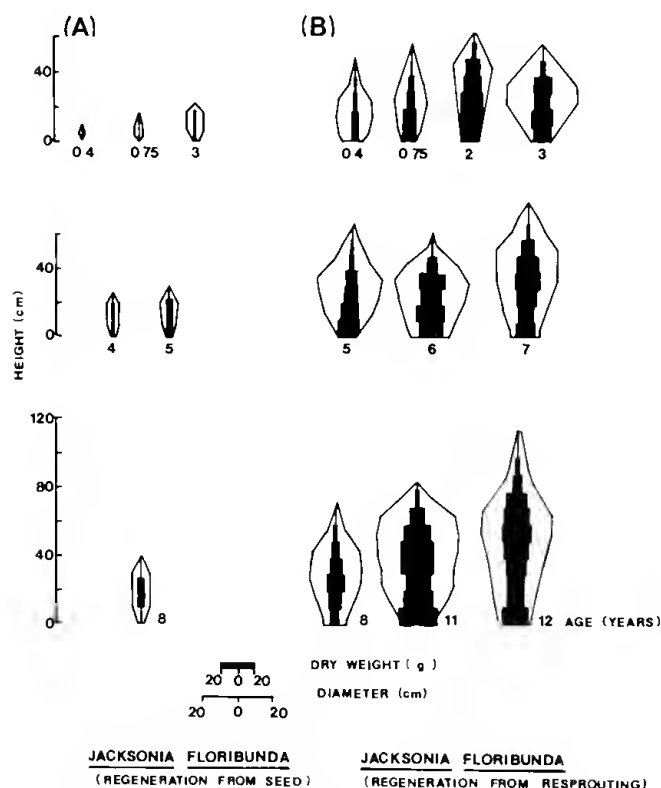


Figure 5.—Mean shrub dimensions of *Jacksonia floribunda* seedlings (A) regenerating individuals (B) following fire.

There are inherent difficulties in interpretation of data on biomass of surviving plants of a resprouter species across a sequence of sites because the mean age of survivors of one population may be very different from that of another site. This is especially so if earlier fires or other environmental events have given very different patterns of recruitment at the sites in question. The present data accumulated for *Jacksonia floribunda* typify this problem; e.g. the population of plants in the region burned two years prior to sampling had a mean total dry weight of 126 g plant⁻¹ compared with only 79 g⁻¹ in a neighbouring site known to have had an 8 year interval since the last burn (Fig. 5b).

(d) Long-lived resprouting species, regenerating extremely rarely from seed

Rapid regeneration of resprouter species was also demonstrated for two common non-clonal, resprouting species, *Hibbertia hypericoides* (Fig. 6a) and *Hypocalymma xanthopetalum* (Fig. 6b). These two species are exceptionally common members of the deep sand communities of the Northern Sandplain (Bell and Loneragan 1985), but, in the authors experience, have never been observed to be regenerating successfully from seed (Bell *et al.* 1984). As with other long lived sprouters, each exhibits highly heterogeneous population structures in terms of number, mass and length of regenerating shoots per plant, tap root diameter, and inflorescence number and fruit reproduction. Unfortunately, the real age of resprouting individuals cannot be assessed with certainty, as growth rings in tap roots are not readily apparent, especially where root stocks have become split or partly destroyed by termites. In any event there is no proof that any growth rings which are present have been produced on a strictly annual basis.

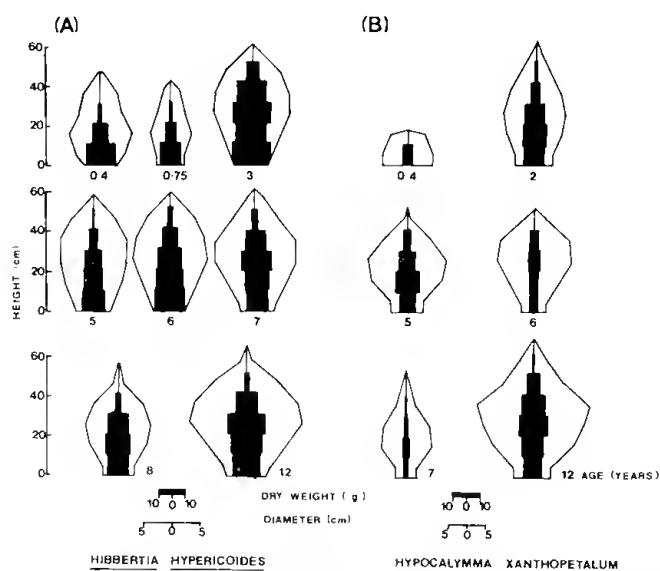


Figure 6.—Mean shrub dimensions of the long-lived autoregenerating species, *Hibbertia hypericoides* (A) and *Hypocalymma xanthopetalum* (B) following fire.

These two long-lived resprouting species showed essentially similar habit to resprouting *Jacksonia floribunda*, and, regardless of size and age, mean diameters of their above ground stems were consistently greater than that of the earlier-mentioned seed regenerating species. In contrast to seeders, resprouters gained dry matter most rapidly over the first three years after a fire (Fig. 6), and with age, showed no tendency for the biomass of their shoots to become concentrated especially towards the top of their shoots.

GENERAL CONCLUSIONS

Species of the Northern Sandplain that regenerate by resprouting appear to have inherent advantages over obligate seeder species in possessing a deeply penetrating massive root stock, from which nutrients can be mobilized to give quick recovery of above ground biomass after fire. The multiple shoots generated from these root stocks give the regenerating shrub a highly characteristic shape, with wide basal diameter and biomass initially concentrated mainly at the base of the plant. Regrowth of resprouters is very rapid in the first 2-3 years after fire followed by a slow and gradual increase over at least the next 14 years.

The seed regenerators studied in the Northern Sandplain shrublands have the same general habit as reported for other fire-sensitive Western Australian species (Baird 1977). Typically a single main stem is established and persists, the root system is typically shallow and of fibrous character (Dodd *et al.* 1984), and biomass is eventually located mostly in the upper reaches of the plant. As shown by the silhouettes of shoot shape and mass distribution described in this paper, those of seeders contrast markedly with those of root-grown resprouters. Moreover, since the seeders tend to establish in spaces between the regenerating crowns of the resprouters, and with time may even overtop the sprouters, both are able to coexist successfully for many years of a post fire interval. Indeed, a properly balanced mix of seeders and sprouters, with essentially complementary shoot canopies and rooting morphologies, is likely to maximize utilization of existing ground cover and resources of water and nutrients. Within this framework also, fast growing

ephemerals such as *Tersonia brevipes* occupy a critical role early in a pyric succession by progressively recovering nutrients released from fire into plant biomass (see Pate *et al.* 1985).

Were it possible to extend information on canopy shape and weight distribution to all major species of some chosen aged community, and to combine this with measurements of density of these species, it would be possible to construct computer-simulated graphical representations of typical biomass structure, and thus assist in predicting how fuel loads are distributed over time and space. Such information would be particularly valuable to a better understanding of fire management of the community.

This study has looked in detail at the responses to fire of only a small sample of species from a highly diverse flora. For the meantime, faced with a paucity of data on regeneration strategies, ecologists must follow a conservative path when using fire as a management tool in these regions (Bell *et al.* 1984, Hopper and Muir 1984). On the one hand, there is the danger that too-frequent fires might result in the loss of those obligatory seed-regenerating species which take an unusually long time to achieve first reproduction (van der Moezel *et al.* 1987). Important apicultural species might well fall within such a category. On the other hand, long periods of fire prevention in kwongan generally lead to the build up of dangerous levels of fuel, and thus increase the possibility of large scale wild-fires sweeping through shrubland and intervening pastureland. Until the Northern Sandplain ecosystem is much better understood, fire management policies should consist of planned mosaics of strategically reduced fuel zones, enclosing less frequently burnt regions, in which already identified, endangered seeder species might be able to survive. Designation of such a policy within National Parks, bee pastures, and specific recreation areas would further ensure sensible planned long-term maintenance of the species and their unique parent communities in the interests of all parties concerned.

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Northern Sandplain Kwongan: effect of fire on *Hakea obliqua* and *Beaufortia elegans* population structure

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Abstract

Individuals of obligatory reseedling species are killed outright by fires and species persistence in the Northern Sandplain shrubland ecosystem requires re-establishment by seed. *Hakea obliqua* and *Beaufortia elegans* share the same basic fire response syndrome—fire sensitivity of mature individuals, lack of seed dormancy and seed storage on the plant, but their adaptations relating to seedling establishment differ. *Hakea obliqua* has few but relatively large seeds and early seedling growth is rapid. *Beaufortia elegans* seedlings grow very slowly by comparison but continued existence in the shrubland ecosystems is ensured by the massive numbers of seed which are dispersed following fire. The massive, synchronous production of small seed apparently satiates seed harvesting predators and sufficient numbers of remaining seeds find conditions of the post-fire habitat favourable for re-establishment of the species.

Season of the burn had considerable impact on the re-establishment of these obligatory reseedling species. Seedling regeneration was most effective following autumn burns and least effective following spring fires. The implications for management in these Northern Sandplain shrublands are that ecologically unfavourable seasons (in this case, winter and spring) should be excluded from prescribed burning regimes if the objective of management is to maintain all components of the pre-fire ecosystem.

Introduction

Fires in the Northern Sandplain shrublands play a major role in floristic structure of the vegetation (Bell and Loneragan 1985). Nearly one-third of the species in this region are killed outright by fire and rely on reseedling to maintain their position in these communities (Bell *et al.* 1984, Bell 1985, van der Moezel *et al.* 1987). Fire also plays an integral role in the reproductive biology of many plants in this environment by inducing synchronous flowering and seed production events (Gill 1981), causing seed release and dispersal (Cremer 1965a) and stimulating the germination of soil-stored seed (Purdie 1977).

The local post-fire persistence of obligate reseedling species is dependent on the events of seed dispersal, seed germination and seedling establishment. Seed store in these species can include both soil- and plant-borne propagules (Vlahos and Bell 1986). Fire stimulates the release of seed from bradysporous species (Cremer 1965b, Cowling and Lamont 1985) and the germination of soil-borne seed (Floyd 1976). Establishment is then dependent on the allocation of seed-stored nutrients and energy for early growth, acquisition of resources for subsequent growth, escape from insect and mammal predation, and survival in competition with other species of the habitat.

Seed contents and metabolic rates can effect establishment success. Northern sandplain shrubs present a range of seed sizes (Pate and Dell 1984) and early growth rates can vary enormously. Population densities following fire can also be strongly influenced by seed predators. Ants have been reported to collect up to 80% of the seeds shed following fire in stands of *Eucalyptus delegatensis* (Grose 1960, Cramer 1966). The massive, synchronized release of seed results in satiation of predators and subsequent seed escape (O'Dowd and Gill 1984).

This paper highlights the influence of fire on population densities in two obligatory reseedling species of the Northern Sandplain shrublands, *Hakea obliqua* R.Br. and *Beaufortia elegans* Schau.

The species

Hakea obliqua (Proteaceae) is an erect shrub growing up to four metres tall in the deep sand shrublands of the region surrounding Badgingarra (Beard 1979). It has sharply pointed, terete leaves, 5–8 cm long and 3–4 mm thick. The flowers are white and are grouped in sessile axillary clusters along most of the length of the branches. The fruit is a woody structure measuring approximately 4x3x2 cm and covered by numerous corky outgrowths.

Two hemispherical seeds about 1 cm long and 0.5 cm thick are contained within each fruit capsule. The seeds have membranous wings and corky outgrowths on the convex side which is embedded in the fruit. Flowering generally occurs in early spring and begins when the plants are four years old (van der Moezel *et al.* 1987). Fruits start to accumulate on the plant from this age, remaining closed until opened by the effects of fire. The seeds are not dispersed immediately after fruit dehiscence but are generally held for up to two weeks by an attachment of the tip of the seed wing to the fruit.

The phanerocotylar seedlings (cotyledons exposed from the testa and borne at ground level upon germination) show moderate rates of early seedling growth (Delfs, unpublished data). By mid-October of the first growing season mean seedling weights average about 1 g plant⁻¹. By two years plant weight has more than trebled and until at least 17 years both biomass and height increase linearly with age (Delfs *et al.* 1987). Plants of 17 years since last burn have mean biomass and height of 1440 g and 330 cm, respectively.

Beaufortia elegans (Myrtaceae) is much smaller at maturity in comparison, rarely exceeding 1 m in height (Delfs *et al.* 1987). The species has a dense crown of small (0.5 x 0.2 cm) leaves and pink clusters of flowers borne terminally. Flowering occurs in November and December (van der Moezel *et al.* 1987). Fruits are generally clustered together numbering 5-10 and measure approximately 0.5 x 0.5 cm. Seeds are numerous but small (0.45 g) and are enclosed in the fruit until burnt.

In contrast to *Hakea obliqua*, the seedlings of *Beaufortia elegans* are phaneroepigeal (exposed and elevated above the soil surface). The cotyledons are green and foliar (as are *Hakea obliqua*), but the hypocotyl is not nearly as elongated in *Beaufortia elegans*. The juvenile period in *Beaufortia elegans* is short despite its obligatory reseedling habit. Flowering occurs in less than two years following establishment (van der Moezel *et al.* 1987). Early seedling growth is very slow with seedlings of at least 15 weeks of age weighing less than 0.2 g or 1/40th of the weight of comparable aged *Hakea obliqua*. By two years mean plant weights average approximately 0.35 g and reach approximately 75 g after 17 years (vs 1440 g for 17 yr old *Hakea obliqua*) (Delfs *et al.* 1987).

Methods

Population densities for *Hakea obliqua* and *Beaufortia elegans* were determined from a range of sites of known age since last burn in the vicinity of the junction of the Brand Highway and the Jurien Road (30°14'S, 115°16'E), approximately 20 km north of Badgingarra, Western Australia. Establishment of seedlings was determined in sites burned within the year prior to the winter seed germination period. Five adjoining 10 x 10 m stands burned the previous autumn and spring were sampled to establish the stand seed load of *Hakea obliqua* prior to burning. The number of seedlings established by August and the number of seedlings still surviving after two months growth were recorded. For *Beaufortia elegans* the number of seeds per plant was established from counts made on plants collected in five continuous one metre square quadrats. Seedling establishment density and two-month mortality figures were determined in two 1 m² quadrats.

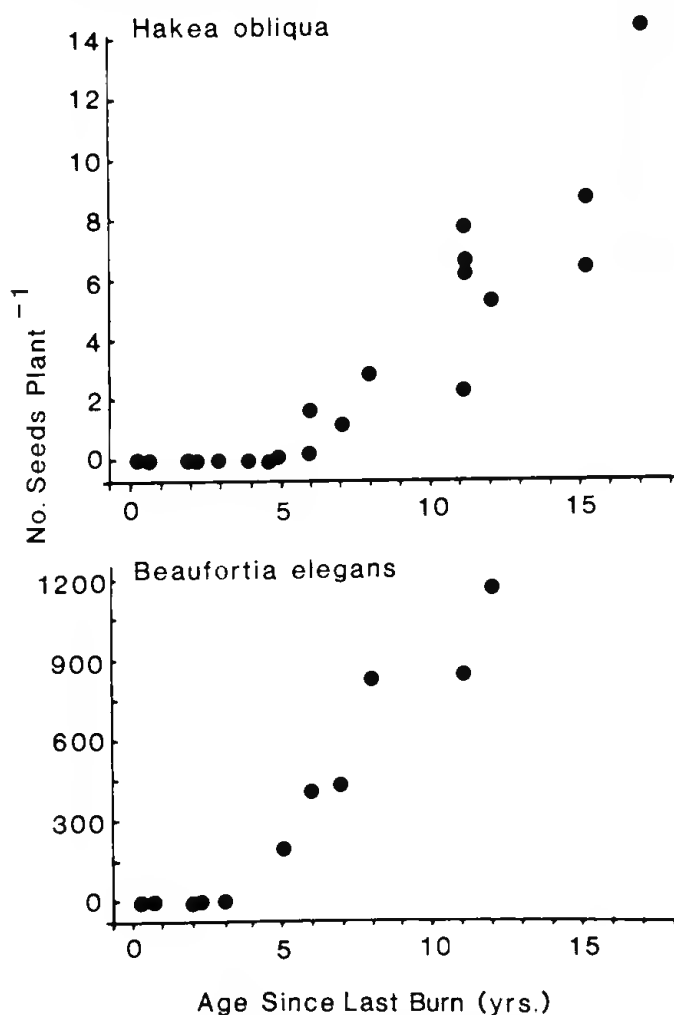


Figure 1.—Plant borne seed store in *Hakea obliqua* and *Beaufortia elegans* in Northern Sandplain shrublands of known age since last burn.

Results

Seed store before fire

Hakea obliqua and *Beaufortia elegans* retain seed in protective fruits until released following death of the supportive tissue. Estimates of the seed store build-up following fire from the site of known age since last burn indicated that the large seeded species, *Hakea obliqua* produced far fewer seeds per plant than the small seeded species *Beaufortia elegans* (Fig. 1). Only the occasional plant of < 5 years held fruit in these two obligatory reseedling species. By about 11 years following fire the accumulated number of seeds per plant in *Hakea obliqua* averaged approximately 6 while the number of seeds stored in *Beaufortia elegans* plants of comparable age was more than 800.

Seedling recruitment following fire

Estimates of seed density prior to the burns and seedling density following fire indicate that *Hakea obliqua* re-establishes a higher proportion of available seed compared with *Beaufortia elegans* (Table 1). *Hakea obliqua* might be expected to establish approximately one seedling from seven plant-stored seed while *Beaufortia elegans* might be expected to establish only one in twelve. Seed freed from fruits by hand have high rates of germination (98% in *Hakea obliqua*, 96% in

Table 1

Population recruitment in *Hakea obliqua* and *Beaufortia elegans* from recently burned sites in the Northern Sandplain shrublands.

Species	Burn site	Age before fire	Adult plants pre-fire ha	Seeds pre fire ha	Seedlings post-fire ha	Percentage of seed establishment	Percentage of pre-fire population
<i>Hakea obliqua</i>	Autumn	>15	700	23 520	3 800	16	543
<i>Hakea obliqua</i>	Spring	11	3 640	6 400	860	13	24
<i>Beaufortia elegans</i>	Autumn	>15	28 000	29 600 000	2 354 000	8	8 407

Beaufortia elegans) (J.C. Delfs, unpubl.). Seed germination occurs within a week of imbibition and without artificial treatments (J.C. Delfs, unpubl.). Apparently large numbers of seed are predated between the time of the fire and the first significant rainfalls of late autumn and winter. The very much larger populations of *Beaufortia elegans* resulted from the much greater pre-fire density. In *Hakea obliqua* the recruitment of new seedlings was very much higher in the region burned in autumn only a few months prior to the winter rains. In the region burned the previous spring, however, the *Hakea obliqua* population was only one-fourth the density of the pre-fire condition.

In the interval between initial counts and density measurements after two months, little mortality had occurred. In two separate sites within the autumn burn, mortality was less than 10% in the first two months (Table 2).

Table 2

Seedling mortality of *Beaufortia elegans* in early months following establishment.

Site no	Adults pre-fire per m ²	Seedlings post-fire	Survival after 2 months
1	8	1 491	97%
2	10	863	90%

Discussion

Species comparisons

Retention of seed on the plant until affected by fire is a strategy adopted by many species present in Australian plant communities (Gill 1981). Delayed dehiscence (bradyspory) is common in species from the families Proteaceae, Myrtaceae and Casuarinaceae (Gardner 1957, Specht *et al.* 1958). A fire is usually required for seed release but dehiscence may also occur when the woody fruit is dehydrated (Gill and Groves 1981). Species which retain seed until firing, such as *Hakea obliqua* and *Beaufortia elegans*, can exploit the open, well-lit, nutrient-rich, pyrogenic seed bed. Seeds accumulate on the plants during the inter fire period, then following post fire release and subsequent establishment ensure the survival of the species for the period until the next fire as both these species do not resprout following fire.

The comparatively large seed of *Hakea obliqua* germinates quickly following the first rain and growth is relatively rapid during the first growing season following fire. The proportion of seedlings surviving the first summer drought might be expected to be high in this species compared to the populations of the small seeded, slow growing *Beaufortia elegans*.

In California chaparral, moisture conditions in burned areas are less favourable than in unburned control areas (Christensen and Muller 1975). Also, mineral nutrient changes which accompany the fire have little or no effect

on post-fire germination responses but subsequent growth and survival on burned areas is thought to be enhanced by better nutrition and reduced grazing pressure. Summer conditions in the Northern Sandplains can be very dry, hot and windy; conditions most likely to be very detrimental to first-year seedlings. Seedlings which develop deep roots rapidly might be expected to have an advantage in preventing summer season desiccation.

Beaufortia elegans appears to have opted for the production of very large numbers of seed of small size. This massive, synchronous reproductive event has possibly evolved in relation to seed predation. Ants predate or bury large numbers of seed (Briese and Macauley 1981). The large numbers of seed released into the habitat following fire results in satiation of predators and subsequent seed escape (O'Dowd and Gill 1984). Summer mortality might be expected to be comparatively greater due to the much smaller first-growing season size of *Beaufortia elegans* (Delfs *et al.* 1987). Although only 8% of the seed store of an area resulted in seedling establishment, less than 1% of the resulting germules would ultimately need to survive to replace the parent population.

Satiation of seed predators has been shown to be operative in the ultimate seed escape and germination of *Eucalyptus delegatensis* in the A.C.T. (O'Dowd and Gill 1984) and *E. incrassata* in north-western Victoria (Wellington and Noble 1985b). Successful post-fire population maintenance in *Beaufortia elegans* seems to rely on predator satiation and ultimately a safe site (*sensu* Harper 1977) where nutrients, light and moisture conditions are favourable to supplement the characteristically slow growth rate of this species.

Both *Hakea obliqua* and *Beaufortia elegans* share the same basic fire response syndrome-fire sensitivity in the adult, lack of prominent seed dormancy and seed storage on the plant. This adaptive strategy is advantageous when the fire frequency occurs at intervals longer than the primary juvenile period but shorter than the life span of the plant. *Beaufortia elegans* is capable of flowering in the second growing season while *Hakea obliqua* usually requires at least three full growing seasons before flowering in the fourth spring (van der Moezel *et al.* 1987). Plants in the site known to be at least 17 years since last burn were all vigorous indicating that the life span of both these species is probably considerably longer than 17 years. The natural frequency of burning in the Northern Sandplain shrublands is suspected to be of the order of 25 years (Bell 1985). Under the natural frequency of burning a significant buildup of plant-borne seed reserves would occur. Maintenance of population numbers would then depend on habitat conditions, especially in the first year following the fire.

In addition to the size of the seed reserves before episodic fires, the population dynamics of these species will also be highly dependent on rates of seed loss following dispersal and before germination and early

seedling mortality. Neither *Beaufortia elegans* or *Hakea obliqua* seed appeared to germinate in the region of the spring burn before the following winter. The seeds, generally dispersed in the first month following a fire, were, therefore, susceptible to seed predation for approximately 8 months prior to the first winter rainfalls. A considerable fire season difference in the proportion of *Hakea obliqua* seeds released which actually lead to established seedlings the following winter was observed. Seed predators are suspected of causing the reduced recruitment following the spring burn. Seed harvesting ants were the main cause of seed loss between dispersal and germination in *Eucalyptus incrassata*, a Victorian mallee with fire-induced seed fall (Wellington and Noble 1985a, 1985b). Seed predation was also the major cause of limited recruitment of South African bradysporous species (Bond 1984).

Seedling mortality

Early mortality was minimal in *Beaufortia elegans* despite highly dense seedling stands. In Cape Province, South Africa, post-emergence seedling predation tends to be minimal in burned areas in contrast to areas of more mature shrubland where seedling predation can be very heavy (Bond 1984). This generalization also appears to apply to the Northern Sandplain. Seedling loss in shrubland habitats can be considerable. Several studies have documented high seedling losses in the first year or two after fire (Horton and Knaebel 1955, Hanes 1971, Wellington and Nobel 1985a). The losses have most often been attributed to competition and drought stress (Schultz *et al.* 1955, Hanes 1977, Christensen and Muller 1975). Density independent mortality of seedlings of *Hakea obliqua* and *Beaufortia elegans* would tend to be high during the first drought season. Density dependent mortality might be expected later in the life cycle of these species. Senescence in these species due to factors related merely to age has not been observed in these species due to the lack of long unburned regions in the study area.

Season of burn

Season of burn appears to have a considerable impact on the continuing success of obligatory reseeders in the Northern Sandplain. Seedling regeneration is most effective following autumn burns; least effective following spring burns. The seasonal differences are due: 1) to the length of time for predation of dormant seeds before the winter germination period and 2) mortality of seedlings due to the competitive advantage provided to the rapidly-resprouting species by the longer interval between the spring burn and germination compared to the autumn burn to winter germination interval. Winter and spring burns are clearly unfavourable for the maintenance of obligate reseeders in the shrublands of this region.

The implications for fire management of the Northern Sandplain and the problems that arise are fairly clear. If the objective of management is to maintain *all* the species present, it is imperative that the prescribed burning seasons should be strictly defined to exclude ecologically unfavourable seasons. Prescribed burning events can then be defined by the opportunity of suitable weather conditions in the ecologically favourable season. Aspects of the buildup of fire fuels are currently being studied (eg. Schneider and Bell 1985), however, fire behaviour studies in the Northern Sandplain shrublands should be a priority for future research. Until further knowledge of the reproductive strategies of shrubland species is documented a conservative path of fire

management should be followed (Hopper and Muir 1984). For the Northern Sandplain, late summer and autumn appear to be the ecologically most favourable season for prescribed burns. Fires during these seasons, however, have the potential to be uncontrollable and fire managers must be provided with guidelines for the safe limits under which prescribed burns may be conducted during these seasons.

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Book Jacobs M R 1955 Growth Habits of the Eucalypts For Timb Bur, Canberra.

Chapter in book Dell J 1983, The Importance of the Darling Scarp to Fauna. In: *Scarp Symposium* (ed J D Majer) *W Aust Inst Technol, Bentley*, 17-27.

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